THE AUSTRALIAN ASCIDIACEA
PART 2, APLOUSOBRANCHIA (1)

PATRICIA KOTT

Kott, P. 1990 6 30: The Australian Ascidiacea Part 2, Aplousobranchia (1). *Memoirs of the Queensland Museum* **29**(1): 1-266. Brisbane. ISSN 0079-8835.

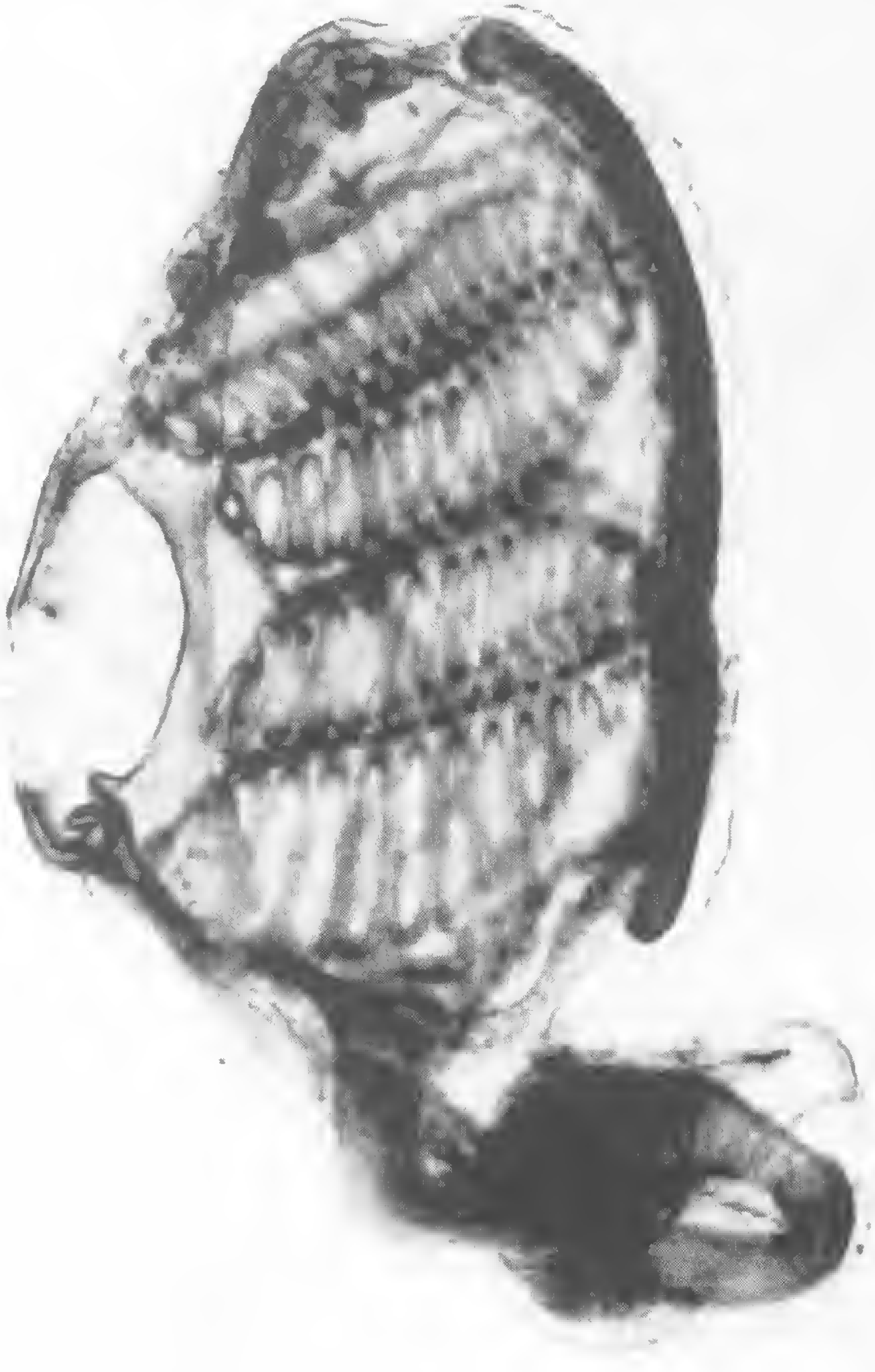
In the primarily colonial suborder Aplousobranchia of the class Ascidiacea (subphylum Tunicata) 106 species in 20 genera in the known family group taxa Cionidae, Diazonidae, Clavelinidae, Holozoidae and Polycitoridae, and the new families Pycnoclavellidae and Stomozoidae are now known to occur in Australian waters. Forty-nine species and 5 genera are also new. Familial and generic (including larval) characters are reviewed and revised; and dichotomous keys are presented for all taxa.

Most of the families are diverse and well represented in Australia. Their phylogenetic relationships and those of some of the genera discussed in this part are obscure. In some cases (e.g. *Sigillina*) evidence from larval adhesive organs conflicts with relationships deduced from adult morphology. There is, moreover, a degree of parallel evolution and convergence in zooid and colony form (apparently directly related to the development of cloacal systems) that often obscures phylogeny. Even in the one genus, *Eudistoma*, which is especially well represented in Australian waters, there is a range of species that reflect most of the stages in the evolution of colonial systems and colony integration, from independently opening zooids to the presence of cloacal cavities and apertures. The anterior diversion of the first row of stigmata along the mid-dorsal line in *Pycnoclavella* and in *Eudistoma* and other polycitorids is another convergent character associated with size reduction and simplification of zooids. It cannot be regarded as a significant character at higher taxon level.

However, the position and shape of the stomach and the length of the oesophagus and duodenum are newly recognised plesiomorphic characters contributing to the definition of a number of genera, as do the arrangement and course of longitudinal body muscles. The site where fertilisation takes place is found to be of significance in defining Pycnoclavellidae but is unexpectedly variable in certain genera of the Polycitoridae.

The geographic affinities of the majority of known species appear to be with tropical rather than subantarctic fauna. Indigenous species are most common in the temperate waters of the southern coast of the continent although there are also some tropical species that appear to be indigenous. ☐ *Indo-West Pacific, Ascidiacea, Aplousobranchia, Cionidae, Diazonidae, Clavelinidae, Pycnoclavellidae, Holozoidae, Polycitoridae.*

Patricia Kott, Queensland Museum, PO Box 300, South Brisbane, Queensland, 4101, Australia; 28 June 1989.



Frontispiece: a juvenile vegetative zooid of the aplousobranch ascidian *Sycozoa pulchra*, showing the posterior gut loop characteristic of the suborder. Branchial tentacles can be seen just inside the incurrent aperture at the top of the pharynx. Two pairs of rows of stigmata perforate the pharynx, and the bilabiate anus opens into the atrial cavity near the rim of the large excurrent aperture. Incipent male follicles can be seen in the gut loop, just behind the oval stomach.

CONTENTS

Introduction, 4
Acknowledgements, 5
Collection and Examination of Aplousobranch Ascidians, 6
Annotated Glossary, 7

APLOUSOBRANCHIA, 18

CIONIDAE, 20
Ciona, 21
  C. intestinalis, 21

DIAZONIDAE, 24
Rhopalaea, 25
  R. crassa, 26
  R. tenuis, 29
Pseudodiazona, 30
  P. claviformis, 31

CLAVELINIDAE, 33
Clavelina, 35
  C. arafurensis, 38
  C. australis, 39
  C. baudinensis, 41
  C. cylindrica, 42
  C. dagysa, 45
  C. fecunda, 47
  C. meridionalis, 48
  C. mirabilis, 50
  C. moluccensis, 51
  C. nigra n.sp., 53
  C. oliva n.sp., 55
  C. ostrearium, 57
  C. pseudobaudinensis, 58
  C. robusta n.sp., 61
Nephtheis, 63
  N. fascicularis, 63

PYCNOCLAVELLIDAE n.fam., 66
Pyncnoclavella, 67
  P. arenosa, 69
  P. aurantia n.sp., 71
  P. detorta, 71
  P. diminuta, 73
  P. elongata n.sp., 76
  P. tabella n.sp., 77
Euclavella n.gen., 79
  E. claviformis, 79

HOLOZOIDAE, 81
Sigillina, 84
  S. australis, 87
  S. cyanea, 89
  S. fantasiana, 92
  S. grandissima n.sp., 93
  S. mjöbergi, 96
  S. nigra, 98
  S. signifera, 100
Polydistoma n.gen., 101
  P. fungiforme n.sp., 102
  P. longitube, 104
Hypodistoma, 105
  H. deerratum, 106
  H. mirabile, 108
Distaplia, 109
  D. australiensis, 113
  D. cuscina n.sp., 115
  D. dubia, 116
  D. florida n.sp., 118
  D. muriella n.sp., 119
  D. pallida n.sp., 121
  D. prolifera n.sp., 122
  D. racemosa n.sp., 124
  D. regina n.sp., 125
  D. retinaculata n.sp., 125
  D. stylifera, 127
  D. tokioka n.sp., 129
  D. violetta n.sp., 130
  D. viridis, 132
Hypsistozoa, 133
  H. distomoides, 134
Neodistoma n.gen., 135
  N. mammillatum n.sp., 135
Sycozoa, 137
  S. brevicauda n.sp., 140
  S. cavernosa n.sp., 142
  S. cerebriformis, 143
  S. murrayi, 146
  S. pedunculata, 147
  S. pulchra, 149
  S. seiziwadae, 152
  S. sigillinoides, 153

STOMOZOIDAE n.fam., 156
Stomozoa 157
  S. australiensis n.sp., 157
  S. bellissima n.sp., 159

POLYCITORIDAE, 162
Polycitor, 165
  P. annulus n.sp., 165
  P. calamus n.sp., 167
  P. cerasus n.sp., 168
  P. circes, 169

P. emergens n.sp., 170
P. giganteus, 171
P. nubilus n.sp., 174
P. obeliscus, 175
P. subarborensis, 175
P. translucidus, 176
Cystodytes, 178
C. dellachiajei, 179
Polycitorella, 183
P. coronaria, 184
P. orientalis n.sp., 187
Eudistoma, 188
E. amplum, 194
E. anaematum n.sp., 196
E. angolanum n.sp., 197
E. aureum n.sp., 199
E. bulbatum n.sp., 200
E. carnosum n.sp., 201
E. constrictum n.sp., 203
E. eboreum n.sp., 205
E. elongatum, 205
E. gilboviride, 206
E. glaucum, 208
E. globosum, 210
E. gracilum n.sp., 211
E. incubitum n.sp., 212
E. laysani, 214
E. maculosum n.sp., 216
E. malum n.sp., 217
E. microlarvum n.sp., 218
E. muscosum nom. nov., 220
E. ovatum, 222
E. pratulum n.sp., 224
E. purpureum n.sp., 225
E. pyriforme, 226
E. reginum n.sp., 228
E. sabulosum n.sp. 229
E. superlatum n.sp., 229
E. tigrum n.sp., 231
E. tumidum n.sp., 232
Exostoma n.gen., 233
E. ianthinum, 234
Brevicollus n.gen., 236
B. tuberatus n.sp., 237

The following account (part 2 of a review of the Australian ascidians) treats species of the families Cionidae Lahille, 1887, Diazonidae Seeliger, 1906, Clavelinidae Forbes and Hanley, 1848, Holozoidae Berrill, 1950, Polycitoridae Michaelsen, 1904, and the new families Stomozoidae and Pycnoclavellidae. These families, together with Polyclinidae Milne Edwards, 1842 and Didemnidae Giard, 1872 (yet to be treated), comprise the 9 presently recognised families of the suborder Aplousobranchia Lahille, 1887. It is one of the two suborders in the order Enterogona, the other being the Phlebobranchia.

The classification and phylogeny of the suborders Phlebobranchia and Stolidobranchia (the only suborder of the order Pleurogona) are reviewed and revised in part 1 of this work (Kott 1985), which also includes accounts of the species of these taxa that occur in Australian waters, guides to their identification and a discussion of their biogeography.

In the following account of the Aplousobranchia, aspects of larval as well as adult morphology have been invoked to determine phylogenetic affinities. Definition of polyphyletic assemblages such as the Clavelinidae and Polycitoridae have been adjusted in order to arrive at monophyletic groupings wherever possible.

Aplousobranch families are separated from one another primarily on the basis of their respective replicative processes, supported by aspects of colony, zooid and larval morphology. Accordingly, the new family Pycnoclavellidae is erected to accommodate genera formerly included in the Clavelinidae. In many taxa the replicative process is not known and, as for the new family Stomozoidae, it has been deduced on the basis of colony and adult morphology. Sometimes evidence from larvae conflicts with a phylogeny based on these deductions. In particular there is uncertainty regarding the family affinities of *Sigillina*, *Hypodistoma* and *Polydistoma* n.gen.; *Sigillina mjöbergi*; and *Cystodytes*, *Polycitorella*, and the new genus *Brevicollus*.

As in Part 1, the following account of aplousobranch families is based on the collections of all Australian and some American and European museums. It includes many thousands of newly recorded specimens recently collected by the author and her colleagues. The general morphology of colony, zooid and, in most cases, the larvae have been examined and recorded. The histology of these organisms has not been considered in this work.

All specimens for which the registration number is cited have been examined in connection with the present work. Where a colony is registered in 2 institutions, the second number (in italics) refers to a sample part only.

Abbreviations used to indicate the institution in which specimens are lodged are as follows: **AM**, Australian Museum, Sydney, New South Wales; **BM**, British Museum (Natural History), London, UK; **MHN**, Muséum Nationale d'Histoire Naturelle, Paris, France; **OM**, Otago Museum, Dunedin, New Zealand; **QM**, Queensland Museum, Brisbane, Queensland; **SAM**, South Australian Museum, Adelaide, South Australia; **TM**, Tasmanian Museum, Hobart, Tasmania; **MV**, Museum of Victoria, Melbourne, Victoria; **NTM**, Northern Territory Museum, Darwin, Northern Territory; **WAM**, Western Australian Museum, Perth, Western Australia; **USNM**, US National Museum of Natural History, Smithsonian Institution, Washington DC, USA; **ZMA**, Zoological Museum of Amsterdam, Amsterdam, Netherlands; **ZMC**, Zoological Museum Copenhagen, Copenhagen, Denmark.

ACKNOWLEDGEMENTS

The many colleagues who have encouraged my studies of the Ascidiacea from 1949 are referred to in Part 1 (Kott 1985). Emeritus Professor C. Burdon-Jones deserves special thanks for his ongoing support and practical assistance with this part of the project. Dr Robin Millar formerly of the Scottish Marine Biological Association, Oban, Scotland also continues with his encouragement and interest. The Queensland Museum Board through the Director, Dr Alan Bartholomai, continues to give its support to this project.

Much of the newly recorded material was taken in the course of major surveys of the fauna of the Australian continental shelf including the North West Shelf and Kendrew Islands (Dr Barry Wilson, Ms Shirely Slacksmith and Ms Loisette Marsh of the Western Australian Museum, supported by Australian Marine Science and Technologies and Crown of Thorns Committee grants); the Great Australian Bight, and Spencer and St Vincent Gulfs (Mr Scoresby Shepherd, Mr Nigel Holmes and other colleagues of the South Australian Fisheries Department, supported by the South Australian Museum and Australian Marine Science and Technologies grants in connection with sea grass productivity and other programmes); Bass Strait and the Victorian coast (Museum of Victoria supported by an Australian Marine Science and Technologies grants, the Western Port Survey, and various surveys conducted by Mrs J. Watson of Marine Science and Ecology, Victoria), the Great Barrier Reef and the Queensland coast (the north-eastern fisheries survey conducted by Dr G. Goeden of the Queensland State Fisheries Department and Dr Lester Cannon of the Queensland Museum, and the Cleveland Bay survey by Mr Alistair Birtles and Dr Peter Arnold of James Cook University of North Queensland, both supported by Australian Marine Science and Technologies grants, the Abbot Point survey conducted by Professor Cyril Burdon-Jones of James Cook University of North Queensland for Mt Isa Mines, and material collected by Mr E. Lovell while engaged in coral collecting programmes for the Australian Institute of Marine Science).

The author's own collecting has been supported by grants from the Australian Research Grants Committee (D65/15386 1969–71; H64/15386 1975); the Australian Biological Resources Survey (1980–82); and the Australian Marine Science and Technologies Grants Scheme (MST 83/1320 to C. Hawkins and P. Mather). Ms Lucille Cevola-Gillespie and Mr Stephen Cook have been able and conscientious assistants both in the field and in the laboratory. Dr David Parry and Mr Andrew Rozefelds have also helped in the field. Stephen Cook drew most of the black and white figures from the authors sketches. Mrs Peta Woodgate typed the many thousands of words that were involved in the preparation of this manuscript for publication, from first draft to its final stage.

Museum curators who have contributed to the progress of the present study by their prompt attention to requests for loans of considerable parts of their collection are Ms L. Marsh (Western Australian Museum), Mr W. Zeidler (South Australian Museum), Ms S. Boyd (Museum of Victoria), Dr. F. Rowe (Australian Museum), Mr G. Anderson (British Museum, Natural History), Dr E. Rasmussen (University Zoological Museum, Copenhagen), and Dr A. Pierrot Bults (Zoological Museum of Amsterdam). I am grateful to them all. Perhaps my greatest indebtedness is to those photographers (both professional and amateur) who provided images of the living organisms *in situ*, and who have allowed me to use those images to illustrate these volumes. They include Graham Edgar (whose photographs of *Ascidia challengeri*,

A. sydneiensis and *Botrylloides magnicoecus* from Port Davey in Part 1 of this work were wrongly attributed), Paul Fredrickson, Rudy Kuiter, Roger Lethbridge, Ed Lovell, Dave Parry, Ron and Valerie Taylor, Gary Russ, W.H. Sasse, and Jeanette Watson. Most particularly I am grateful to Neville Coleman, Scoresby Shepherd and Nigel Holmes whose careful indexation of image to the actual preserved specimen has removed the possibility of error that occurs when identification based only on photographs is attempted.

COLLECTION AND EXAMINATION OF APLOUSOBRANCH ASCIDIANS

Generally species of the suborder Aplousobranchia are more difficult to collect and preserve than are phlebobranch or stolidobranch species. There are several reasons:

1. the test that surrounds the zooids, or in which they are embedded is relatively soft, and this together with the large cloacal spaces (when they are present) make colonies vulnerable to damage and distortion.
2. Possibly because the test is relatively soft and lacks the fibrous, leathery properties of most stolidobranch species, it does not usually adhere firmly by a small part of the surface, or form tough rooting systems. Thus colonies are seldom upright and more often they grow two-dimensionally, over flat, hard substrates to which extensive areas of basal surface or extensive stolon systems form such firm attachments that colonies are difficult to remove. In these cases the colony, lacking other skeletal elements, has the advantage of the substrate to support it. Exceptions are in genera where species are sometimes (*Sigillina*), or always (*Sycozoa*) stalked. In the latter genus the stalk often is long and leathery.
3. Zooids are invariably small and usually muscular. They need careful narcotisation to ensure that their structure is not obscured by contraction.

Thus the collection of aplousobranch ascidians by dredge results in the sampling of large, firm colonies, such as *Polycitor giganteus*. However the great majority of taxa with delicate test, including those with separate zooids (Diazonidae, Clavelinidae, Pycnoclavellidae) or taxa with small or flat and two dimensional colonies (*Eudistoma*) are not adequately sampled.

On the other hand, although most aplousobranch ascidians occupy cryptic habitats, their bright colours (which usually are not hidden by the ephiphytes or adhering foreign particles that occur in Stolidobranchia) are conspicuous, and have attracted the attention of SCUBA divers. In the past twenty years, collections by hand, using SCUBA equipment has demonstrated a diversity in the Australian aplousobranch fauna that formerly was not recognised.

Where possible, to avoid damage, specimens should be removed from the substrate. However, occasionally, the whole or part of the substrate with its adhering ascidians can be collected. Sometimes because of the size of the colony, or the strength of its adhesion, it will be possible to sample only a part. In this case the size of the whole colony and the part of it represented by the sample should be recorded.

As well as physical damage and contraction of the specimens the study and identification of ascidians is made difficult by the loss and rapid oxidation of pigments, following their collection, fixation and preservation. Colour notes should be made and colour photographs of the living specimen (carefully indexed to the specimen) should be taken if possible. Notes should also be taken on the arrangement of zooids in living colonies for in preserved material this also is obscured by colour changes, and contraction.

Since most aplousobranch ascidians generate acid on lysis of the test cells (Parry 1984, 1987), specimens should be thoroughly washed in seawater after removal from the substrate.

Menthol crystals are an appropriate narcotising agent for ascidians. More rapid relaxation is achieved by using a very weak solution of MS222 (Sandoz Ltd.). A few grains of powder in 5ml seawater was made up as a stock solution. About 2 drops of this solution per 100ml of sea water was found to relax most species rapidly and completely.

When examining colonies with embedded zooids, their morphology, and orientation and arrangement in the colony can be observed in thin inspection slices or wedges cut through the whole radius of a cloacal system or colony lobe, from the cloacal aperture or centre of the lobe to the outer margin, parallel to the long axis of the zooids through whole depth of the colony. To examine them more closely and for dissection, the zooids themselves are often removed more easily from these inspection slices than by any other method of pulling them from the colony. Very small zooids can be examined and dissected in a drop of glycerol on a microscope slide. Sometimes they need to be stained before this is done. Most taxa of the suborder Aplousobranchia are viviparous and embryos are found incubating in the colony. These can be examined by staining, clearing and mounting whole.

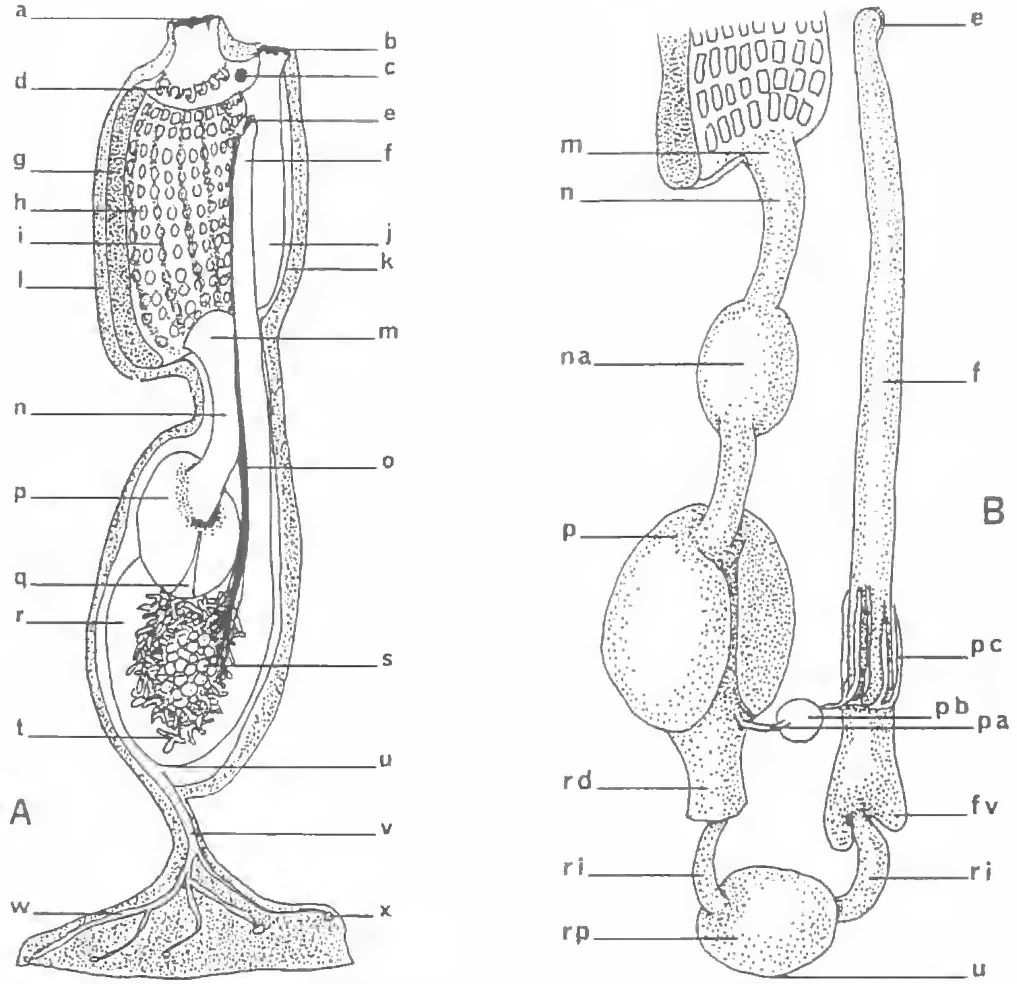


FIG. 1, Ascidian morphology (diagrammatic): A, stalked, solitary individual divided into thorax (**a–m**) and abdomen (**m–u**); B. gut loop, showing subdivisions, associated organs, descending (proximal) limb (**m–u**) and ascending limb (**u–e**). Symbols: **a**, branchial aperture; **b**. atrial aperture; **c**, neural complex; **d**, branchial tentacles; **e**, anus; **f**, rectum; **fv**, rectal valve; **g**, endostyle; **h**. stigmatum; **i**, internal longitudinal vessel; **j**, atrial cavity; **k**, parietal body wall; **l**, test; **m**, oesophageal opening; **n**, oesophagus; **na**. prestomach (found only in some *Clavelina* spp.); **o**, vas deferens; **p**, stomach; **pa**, gastro-intestinal duct; **pb**, gastric vesicle; **pc**, tubules of gastrointestinal (pyloric) gland; **q**, gastric suture line; **r**, intestine; **rd**, duodenal region of gut; **ri**, mid-intestine; **rp**, posterior stomach; **s**, ovary; **t** testis; **u**, pole of the gut loop, **v**, vascular stolon; **w**, test vessels; **x**, terminal ampullae.

ANNOTATED GLOSSARY

The morphology of aplousobranch ascidians (Figs 1,2) is discussed, and the terms and conventions used in this work are defined below. The morphology of the Ascidiacea has been reviewed by Berrill (1950). Goodbody (1974) has reviewed the physiology and Millar (1971) the biology of the group. The annotated glossary in Kott (1985) should be used in conjunction with the following entries:

adhesive organs: epidermal structures at the anterior end of the larval trunk. Larger larvae have 3 in a triradial arrangement, but in the small larvae of the Polycitoridae, Polyclinidae, and Didemnidae they are in a median vertical row. Occasionally there are only 2 adhesive organs (*Pycnoclavella* spp., *Sigillina* spp., *Euherdmania* spp.). In some Didemnidae (e.g. *Diplosoma multipapillata* Kott, 1980) and Polyclinidae (e.g. *Aplidium triggiensis* Kott, 1963; 1976) the presence of more than 3 adhesive organs is probably an adaptive response to environmental pressures. The most simple organs are non-everting conical ones found in the small larvae of *Ciona*, the Diazonidae, and solitary phlebobranch and stolidobranch ascidians which, with the exception of a few *Polycarpa* spp. (see Kott 1985) and some *Molgula* spp., are all oviparous. With the exception of the Diazonidae, colonial species of all suborders have viviparous larvae with more complex everting adhesive organs.

Cloney (1977), in the only study on the fine structure of the adhesive organs of ascidians, investigated the adhesive organs of *Distaplia occidentalis* Bancroft and *Diplosoma macdonaldi*. They are entirely ectodermal in both species, and are essentially the same, consisting of an axial cone from the centre of a cup-shaped protrusion at the end of a stalk. The larval haemocoelic cavity continues up into the walls of the cup separating its outer (marginal) wall from the inner (parietal) wall. The cup rim has myoepithelial cells (which contract during the eversion of the axial cone) and anchor cells which hold the larval test firmly in place against the ectodermal epithelium. The parietal wall of the cup and outer wall of the axial cone contains secretory cells (collocytes) which produce adhesive material. The core of the axial cone contains columnar epithelial cells which extend the whole length of the cone and have apical processes extending into a terminal hyaline cap that protrudes through an opening in the larval test and forms the initial attachment to the substrate. Subsequently adhesive material is released from the secretory cells of the surface of the axial cone which is extruded through the test. The eversion of the axial cone and the attachment of the larva to the substrate is a complex process also involving fibrous lamellae from the concavity of the adhesive organ, between the axial cone and the parietal wall of the surrounding cup (see Cloney 1977).

In Aplousobranchia, there are (at least) 5 basic types of everting adhesive organs, including the simple axial cones described by Cloney (1977) *viz*:

1. Invaginated tubes in Pycnoclavellidae, *Euherdmania*, and *Sigillina mjöbergi*.
2. Simple axial cones composed of central columnar and peripheral cells in the centre of epidermal cups in which the haemocoel protrudes between parietal and marginal layers of cells, as described by Cloney (*loc. cit.*). These appear similar in Clavelinidae, Stomozoidae n.fam., *Sycozoa*, *Distaplia*, *Hypsistozoa*, *Polycitor*, *Eudistoma*, *Cystodytes*, *Polycitorella*, Polyclinidae and Didemnidae. Adhesive organs of this type have stalks of various lengths, from short and thick (in Clavelinidae and Holozoidae) to long and narrow (in some Polycitoridae, and in Polyclinidae and Didemnidae). The axial cones are shallow and sessile in wide ectodermal cups in Clavelinidae and Stomozoidae; conical and constricted around their base in deep ectodermal cups in *Distaplia*, *Sycozoa* and related genera in the Holozoidae, and in *Cystodytes* and *Polycitor* (Polycitoridae); wide, flat-topped and mushroom-shaped with a pronounced constriction around the base and shallow ectodermal cups in *Eudistoma* and *Polycitorella* (Polycitoridae).
3. Complex flat-topped axial platforms and ridges composed of arborescent groups of columnar cells that resemble those of *Eudistoma* to some extent, but are larger and are depressed into the ectoderm (rather than stalked). These occur in *Sigillina* and *Hypodistoma*. It is possible that they will be found also in *Polydistoma* n.gen.
4. Cloney (1977) refers to a thick-walled axial vesicle filled with adhesive in larvae of *Eudistoma ritteri* Van Name and *E. molle* Ritter (see Van Name 1945). Adhesive organs of species of *Polycitor*, *Eudistoma* and *Exostoma* n.gen. in the present collection are stalked, and have flat-topped, rather than conical, axial protrusions with the usual columnar and peripheral cells (see 2., above).
5. The tulip-shaped sessile adhesive organs of *Brevicollus tuberatus* appear another type. Their long, double-layered walls may be the homologue of the ectoderm cup of other forms, but they do not contain an axial protrusion of any sort, and the deep elliptical concavity has apparently filamentous lamellae resembling those in the sulcus between the parietal wall of the cup and the axial cone of *Distaplia* (Cloney 1977). The relationship of these with other adhesive organs is not apparent.

apertures: The incurrent (or branchial) aperture and the excurrent (or atrial) aperture are the two openings of the ascidian body. The rim of the branchial aperture is divided into 6 lobes in most aplousobranch taxa except in the Clavelinidae and Pycnoclavellidae (in which it is smooth) and in *Sycozoa* (in which the lobes are much reduced). The incurrent stream of water, generated by the cilia lining the pharyngeal perforations (stigmata), enters the branchial sac through the branchial aperture, which always opens directly to the exterior. The excurrent water that has been strained through the branchial wall, together with faeces and reproductive products expelled into the atrial cavity, leave the zooid through the excurrent (or atrial aperture). This opens directly to the exterior in the Diazonidae, Clavelinidae, Pycnoclavellidae, *Sigillina*, *Polydistoma* n. gen., Stomozoidae, Polycitoridae (with the exception of *Exostoma*), and Euherdmaniinae. The excurrent water is expelled indirectly, through a cloacal cavity with a limited number of openings to the exterior, in Holozoidae (with the exception of *Sigillina* and *Polydistoma* n.gen.), *Exostoma* n.gen., Polyclininae and Didemnidae.

In the former group of taxa the atrial aperture is always 6-lobed but in the latter group only *Exostoma* n.gen., and *Hypodistoma* have 6-lobed atrial apertures. The others have an upper lip, sometimes subdivided, which inserts into the test around or along the sides of the cloacal cavity or its apertures. The sides and posterior border of the atrial apertures of these genera usually are smooth.

The number (6) of lobes around the rims of the apertures is relatively stable in Aplousobranchia. The only exceptions (as described above) are where atrial apertures are adapted to open into cloacal cavities, and where the rims of the openings are smooth (Clavelinidae and Pycnoclavellidae). There is less stability in this character in other suborders. Phlebobranchia have 6 or more atrial lobes and usually more branchial lobes. Stolidobranchia basically have 4 branchial and 4 atrial lobes (Styelidae, Pyuridae), or 6 branchial and 4 atrial lobes (Molgulidae), although modifications can occur that change these numbers.

When zooids open separately surface features of the test often separate incurrent and excurrent streams of water by directing them away from one another, or by raising cloacal apertures above the branchial ones (Kott 1989).

anal opening, anus: see **gut, gut loop**.

ascending limb of gut loop: see **gut, gut loop**.

asexual reproduction: see **cloacal systems, colonies, epicardium**.

atrial cavity: the cavity, lined by ectoderm, formed (in the Enterogona) by fusion of paired invaginations from the dorsum to surround the sides of the pharynx. Ciliated pharyngeal perforations open into this cavity. In Aplousobranchia the gut loop and gonads are posterior to the cavity and not embedded in the parietal body wall alongside it, as they are in Stolidobranchia and Phlebobranchia.

branchial folds: such as those found in the Stolidobranchia, do not occur in the Aplousobranchia, in which the pharyngeal wall is always flat.

branchial papillae: papillae, vertical to the plane of the pharyngeal wall, which support the internal longitudinal vessels. Both occur in Cionidae and Diazonidae. The minute papillae on the transverse vessels of *Protopolyclinum* Millar, 1960 and *Polyclinum* may be vestiges of the vertical papillae. There are no papillae in other aplousobranch families

branchial sac: the pharynx of an ascidian, perforated by rows of stigmata. In colonial ascidians, as replication becomes more prolific and zooids become more numerous, their progressive reduction in size and increasing simplification is reflected in the branchial sac. In Aplousobranchia numerous stigmata in many rows and internal longitudinal vessels are present only in the Cionidae and Diazonidae, but in other taxa the internal longitudinal vessels are lost and stigmata decrease in number as zooids become smaller. Clavelinidae and *Polycitor* sometimes have relatively numerous stigmata in numerous rows but internal longitudinal vessels are absent. The number of stigmata per row remains relatively high in *Sigillina* and *Pycnoclavella*, although the number of rows is reduced. *Sigillina* has only 3 rows of stigmata and some *Pycnoclavella* spp. have only 2 (see below). Both the number of rows and the number of stigmata per row is most reduced in the small zooids of *Eudistoma*. (See also **branchial papillae, internal longitudinal vessels**).

branchial tentacles: stumpy or tapering endodermal structures, in one or more circles at the base of the branchial siphon. In Aplousobranchia they are always simple without side branches. They occur in more than one circle in many species, *viz*. in Clavelinidae and in *Eudistoma*. *Eudistoma* may have up to 9 circles of tentacles in a wide band at the base of the branchial siphon.

brooding: see incubation of embryos.

budding: see replication.

cloacal cavities, — systems: arrangements of embedded zooids around cloacal cavities in the test, into which their atrial apertures open, rather than opening directly to the exterior. The branchial apertures maintain their separate independent openings directly to the exterior. The degree of integration of the colony can be measured by the form of the systems and the extent to which the zooids are organised into systems. Any cloacal system indicates a fair degree of integration.

The most rudimentary cloacal systems are those in the Polycitoridae (*Eudistoma*, *Polycitorella* and *Cystodytes* but not in *Polycitor*) in which zooids are arranged in circles (Fig. 2c), their atrial apertures toward the centre of the circle where the excurrent streams of water reinforce one another. Sometimes the atrial apertures open into a depression in the centre of the circle (Fig. 2d). This is a forerunner of the most simple cloacal system in which a circle of zooids surrounds an actual cloacal cavity which receives excurrent water from the atrial apertures which open into it. This water leaves the colony through a cloacal aperture (sometimes referred to as a common cloacal aperture) in the surface test that roofs over the cavity (Fig. 2e).

The evolution of cloacal systems includes their extension from circles to ovals, and subsequently to long and sometimes branching systems of canals, which radiate away from the cloacal aperture beneath the surface of the colony. In the highly integrated colonies of *Sycozoa*, long cloacal canals, lined on each side with a row of zooids, extend parallel to one another down the sides of the colony. In Didemnidae, cloacal cavities are sometimes almost continuous spaces that surround the zooids, or clumps of zooids, either at thoracic level, or extending into the lower half of the colony to surround the whole length of the zooids with deep spaces (see Kott 1962). In *Atriolum* and *Leptoclinides* (Didemnidae), *Hypodistoma* (Holozoidae) and *Exostoma* n.gen. (Polycitoridae), long, posteriorly oriented, atrial siphons from the postero-dorsal part of the thorax carry excurrent water to cloacal spaces and canals at abdominal or even posterior abdominal level.

Holozoïdae have a great range in the development of systems. In *Sigillina* the atrial aperture of each zooid opens separately to the exterior, but most species have a degree of integration in the colony. Usually they have a basal stalk and a terminal head with the zooids opening around the head and all facing the same way. Their endostyles (ventral surfaces) are below the dorsal surfaces, the branchial apertures face down toward the stalk, and the atrial apertures are directed upwards, toward the top of the colony (see Kott 1989). Thus, although the colony could be said to comprise a colonial system, cloacal systems are not formed. Similarly the new genus *Polydistoma*, with branchial apertures on the undersurface of the fronds of the colony and the atrial apertures uppermost, can be said to have colonial, but not cloacal, systems. Similar systems are present in certain genera of the Euherdmaniinae (viz. *Ritterella*).

In the Polyclininae (Polyclinidae), most species of the Didemnidae, the holozoid genera *Neodistoma* n.gen. and *Hypodistoma*, and the polycitorid *Exostoma* n.gen., the cloacal systems are extensive, and involve large numbers of small zooids. The shape and size of these cloacal systems and the colonies themselves lack the regularity of those in *Distaplia* and *Sycozoa*, being more affected by environmental factors and age.

In *Distaplia* and *Sycozoa* the disposition of zooids is ordered, cloacal systems are regular in size and shape, and are systematically arranged in the colony, replication is prolific, and gamete production is synchronised. It is probable that *Sycozoa* spp., with certain didemnid species, represent the most highly integrated colonies in the Ascidiacea. In stolidobranch ascidians, cloacal systems occur only in Botryllinae. Sometimes they are comparable with the extensive branching systems found in Polyclininae. Only occasionally (*Botrylloides magnicoecus*) do they achieve the degree of integration that occurs in the *Sycozoa* and in most *Distaplia* spp.

colonial systems: an ordered rather than random arrangement of zooids in the colony. Colonial systems include cloacal systems (see above). In many species of Clavelinidae, Pycnoclavellidae, *Sigillina* spp., *Polydistoma*, Stomozoidae, Polycitoridae and Euherdmaniinae (Polyclinidae), however, in which the zooids maintain their independent atrial aperture direct to the exterior, colonial systems are formed that do not involve a common cloaca. In these systems zooids are regularly arranged, sometimes (but not always) in stalked colonies, with their branchial and atrial apertures co-ordinated with

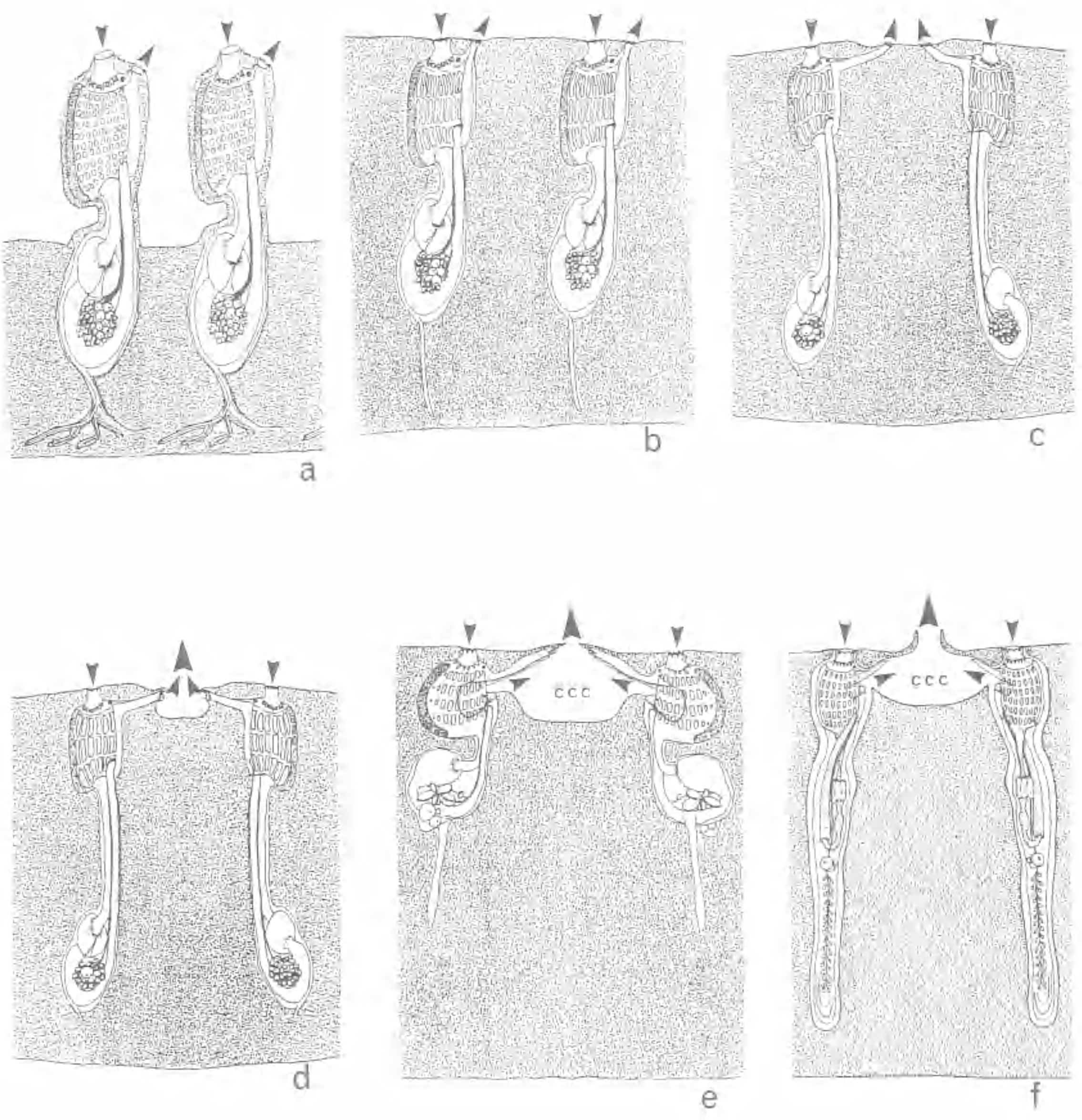


FIG. 2. Evolution of cloacal systems (diagrammatic): **a**, partially embedded zooids, no systems (*Diazona*, *Clavelina* and *Pycnoclavella*); **b**, completely embedded zooids forming colonial, but not cloacal, systems with 6-lobed atrial siphons opening separately to the exterior (*Clavelina* spp., *Nephtheis fascicularis*, *Sigillina* spp., *Polydistoma* n.gen., *Stomozoa*, *Polycitor* spp., *Eudistoma* spp.); **c**, zooids arranged in circles with 6-lobed atrial siphons opening in the centre to form incipient cloacal systems (*Eudistoma* spp., *Polycitorella* spp., *Cystodytes* spp.); **d**, zooids with 6-lobed atrial siphons opening into rudimentary (*Eudistoma* spp.) to extensive (*Hypodistoma* spp., *Exostoma* n.gen.) cloacal cavities; **e,f**, zooids formed into well developed cloacal systems, their wide-lipped excurrent openings often exposing their branchial sacs directly to the long, sometimes branching cloacal canals or cavities, each of which opens to the exterior by a single cloacal aperture, **e**, zooids with gonad in the gut loop (*Distaplia*, *Sycozoa*, Didemnidae), **f**, zooids with gonads in a posterior abdomen (Polyclinidae). Symbols: **ccc**, common cloacal cavity; the arrows show direction of current flow.

respect to environmental factors (such as direction of current flow). There is no indication of even a moderate degree of integration in the colonies of other taxa in the Diazonidae, Clavelinidae and Pycnoclavellidae in which the zooids, although colonial, being joined by basal stolons, or partly (Fig. 2b) or completely embedded, do not form systems.

colonies: With the exception of *Ciona*, certain species of the Diazonidae (*viz. Rhopalaea* spp.), and Clavelinidae (*Clavelina dagysa, C. ostrearium, C. meridionalis, C. viola, C. miniata*), all aplousobranch ascidians are colonial. The zooids that make up the colony are produced by replication of the oozooid (primary zooid) usually following metamorphosis. Sometimes replication begins in the larva, buds being isolated from a vegetative stolon containing an extension of the epicardial sac in the region of the oesophagus (*Sycozoa, Distaplia* and *Hypsistozoa* in the Holozoidae and some Didemnidae), although these buds do not always persist to form definitive zooids (see Berrill 1950; Brewin 1956b). The various budding processes have been summarised by Berrill (1935b, 1950) and Kott (1982b). Replication occurs in all aplousobranch ascidians except *Ciona* and *Rhopalaea*. Watanabe and Tokioka (1973) have shown how the solitary zooids of *Clavelina miniata* develop from buds that subsequently move away from the parent zooid. *Clavelina meridionalis* replicates develop from the vascular stolons in the stalks that persist after degeneration of the parent zooid (see below). Regeneration of thoraces from the oesophageal region of both *Ciona* and *Rhopalaea* may be an early stage in the evolution of the replicative process and the development of colonies in Aplousobranchia (see Kott 1982b; see also **colonial systems, cloacal systems** and **replication**).

descending limb of gut loop: see **gut loop**.

distal: the end of an organ or structure toward which the contents or products move, or which is farthest from the base or point of origin (see also **proximal**).

dorsal lamina, — languets: pointed, triangular projections from the transverse vessels of the branchial sac where they cross over the dorsal sinus. They are in a line parallel and to the left of the dorsal mid-line in most genera of the Aplousobranchia. A plain-edged fold of the pharyngeal wall forming a dorsal lamina as in many families of Phlebobranchia and Stolidobranchia does not occur in Aplousobranchia. Berrill (1950) believes that the presence of dorsal languets is a more primitive condition than the continuous fold.

dorsal tubercle: see **neural duct**.

duodenum: see **gut loop**.

endocarps: thickings or fleshy outgrowths of the parietal body wall that occur often in Stolidobranchia. They are not found in Aplousobranchia.

epicardial sacs, epicardium: paired endodermal sacs that evaginate from the postero-ventral part of the pharynx. In *Ciona* these sacs develop following metamorphosis (see Berril 1950). The left sac envelopes the gut and gonads, and the right one the heart and pericardium. In *Ciona* they maintain their openings into the pharynx, one opening on each side of the mid-line in the ventral part of the retropharyngeal groove. In the Didemnidae, and the genus *Euherdmania* (Polyclinidae), the sacs remain separate from one another. In the majority of other taxa they fuse into a single epicardium which extends along the length of the abdomen (where it is associated with the oesophagus and stomach) to terminate around the pericardium at the posterior end of the abdomen (Diazonidae, Clavelinidae, Pycnoclavellidae, Polycitoridae), and at the end of the posterior abdomen (Polyclinidae with the exception of *Euherdmania*). In *Euherdmania*, as in *Ciona*, one of the 2 sacs is associated with the gut loop in the abdomen. The other extends the length of the posterior abdomen to terminate around the pericardium and heart which, in *Euherdmania*, is in the posterior abdomen (Trason 1957).

Although in Holozoidae, the epicardial sacs are believed to fuse, there are two in *Sigillina grandissima* n.sp. (see below). The left sac lies in the abdomen and, again as in *Ciona*, it is this left sac that terminates over the pericardium. The right sac extends the length of the vegetative stolon as is usual in the Holozoidae where the fused epicardium extends beyond the heart to form a narrow lumen in the vegetative stolon. The presence of the epicardium in the vegetative stolon distinguishes that organ from the large vascular stolon of the Clavelinidae and Pycnoclavellidae.

It was the presence of the epicardium in the vegetative stolon of the Holozoidae that led Caullery (1909) to suggest the stolon was the homologue of the posterior abdomen in the Polyclinidae. However these structures differ, not only in the absence of the gonads and heart from the holozoid stolon, but also in the processes by which they respectively form the replicate zooids that are added to the colonies (see Caullery 1909). In the Didemnidae the sacs are much reduced in length and persist as two small vesicles in the oesophageal region. As in all other groups except Clavelinidae, the epicardium in Didemnidae comprises the regenerative tissue in the replicative process (see Berrill 1935b, 1950).

In Phlebobranchia the embryonic epicardium is the source of the excretory vesicles that lie around the gut loop. In Stolidobranchia the epicardium is probably also involved with excretion (see Berrill 1950, and Saffo 1978 for an account of the kidney in Molgulidae).

excurrent aperture: see **apertures**.

fertilisation: occurs externally in Cionidae and Diazonidae (as in most Phlebobranchia and Stolidobranchia). All other Aplousobranchia are internally fertilised, either in the oviduct or in the atrial cavity (see also **incubation of embryos**).

gastric caecum: a small diverticulum of the stomach which often is present in phlebobranch and stolidobranch ascidians. It is present in juvenile *Ciona* (see Millar 1953a) but not in other aplousobranch taxa.

gastric folds, — ridges: parallel longitudinal glandular swellings in the internal lining; or the folds of the whole stomach wall. These occur in aplousobranch taxa *Ciona*, *Rhopalaea*, some *Distaplia*, and *Polycitor* (see Key to the genus *Polycitor*, below), Stomozoidae n.fam., *Euherdmania*, *Ritterella* and *Aplidium*.

In Stolidobranchia, glandular folds occur in Styelidae and Molgulidae and in some Pyuridae. However, in the latter family *Pyura* has a characteristic, large, branching, liver diverticulum which may take the place of gastric folds. In aplousobranch ascidians there is neither a gastric caecum (as in Styelidae), nor a liver diverticulum (as in the Pyuridae and Molgulidae), nor any other diverticula of the stomach wall other than the gastric folds or ridges that occur in the few taxa referred to above.

Although it is primarily smooth, the stomach wall sometimes is folded into 4, probably as an artefact of its preservation, in *Pseudodiazona*, some *Rhopalaea* (e.g. *R. tenuis*), Clavelinidae, Pycnoclavellidae and *Sigillina*. The stomach wall is completely smooth in *Polydistoma* n.gen. *Hypodistoma*, certain *Polycitor* and *Distaplia*, *Sycozoa*, *Eudistoma*, most *Polycitorella*, *Cystodytes* and *Exostoma* n.gen.

gastric reservoir: see **gastro-intestinal gland**.

gastro-intestinal gland, — connective: as in phlebobranch and stolidobranch ascidians, a gastro-intestinal (or gastric, or pyloric) gland is present in the Aplousobranchia. The gland has tubules that encircle the ascending limb of the gut loop adjacent to the stomach (which is in the descending limb). These tubules join into a single duct (gastro-intestinal connective: Kott 1985) which opens into the distal end of the stomach at its junction with the duodenum. Sometimes the duct expands into a spherical reservoir about halfway along its length.

The gland probably is present in all ascidians (Berrill 1950). It is known to occur in *Ciona*, Perophoridae, Corellidae, Ascidiidae, Styelidae, Pyuridae, Molgulidae, and in Clavelinidae, Holozoidae, Polycitoridae, Polyclinidae, and Didemnidae (see Millar 1953a, Goodbody 1974), although it has not been reported for every species. However it often is very inconspicuous. It is particularly well developed and conspicuous in *Eudistoma* spp., with numerous, long tubules clustered around the outside of the ascending limb of the gut loop.

gonads: Gonads of most aplousobranch taxa are in the abdomen, in or beside the posterior end of the gut loop. Exceptions are Polyclinidae (in which they are invariably in a posterior abdomen behind the abdomen), certain *Distaplia* (in which they are in a posterior abdominal sac that is connected to the side of the abdomen by a narrow neck), and *Hypsistozoa* (in which the gonads are in the top of a posterior abdominal stolon).

Most aplousobranch ascidians are hermaphrodites. They are either protandrous or protogynous, and the zooids in one colony have gonads at more or less the same stage at the one time. For instance, in *Sigillina australis* and *S. mjöbergi* the eggs are fertilised and begin their development before the testis is mature; and in *Distaplia florida* n.sp. and *D. viridis* the testis matures before the ovary. With one exception (*Sycozoa anomala* Millar, 1960), *Sycozoa* colonies are dioecious, at any one time all the zooids being either male or female. Nevertheless it is not known whether or not the colony remains the same sex through its life.

Gonad and gamete size, especially ovaries and eggs, change markedly throughout the Aplousobranchia. *Ciona* produces many small externally fertilised eggs, and so do diazonid species. In other families ovaries are reduced in size as, with replication, the zooids become smaller. Eggs are larger, fewer and internally fertilised as the increasing integration of the colony accommodates incubation of the embryos, either in the zooid or in the colonial test.

Testes also reduce in size with decrease in zooid size, however, they do not reduce quite as markedly as ovaries do; and although follicle numbers are reduced, their size often compensates for this, the male follicles often becoming larger as their number falls (see *Distaplia*). Since the Aplousobranchia are almost universally internally fertilised and viviparous, the concentrations of male gametes in the surrounding waters need to be maintained.

The increase in the number of zooids through replication compensates for smaller gonads in each zooid (see also **incubation of embryos**).

gut, gut loop (Fig. 1b): In aplousobranch ascidians the gut is always entirely posterior to the pharynx. It forms a narrow vertical loop in most taxa except Cionidae, *Hypodistoma*, *Polydistoma* and the Didemnidae in which it forms a more or less horizontal loop. The descending limb of the gut loop in Aplousobranchia is from the oesophageal opening to the point, usually just proximal to the rectum, where the gut reaches the posterior end of the abdomen and turns into the ascending limb at the pole of the loop. The ascending limb of the gut loop runs beside the descending limb to terminate in the anus, opening into the atrial cavity.

The anal opening is well anterior near the base of the atrial aperture in *Ciona* and in the Diazonidae, toward the posterior end of the atrial cavity in most other taxa and usually between the third and fourth or second and third rows of stigmata in Holozoidae and *Eudistoma*, respectively. Only in Pycnoclavellidae is the anal opening at a level with the oesophageal opening, at the posterior end of the atrial cavity.

Subdivisions of the gut found in Aplousobranchia are an oesophagus with or without a prestomach swelling in it, a stomach, a duodenal area, a mid-intestine often with a posterior stomach swelling in it, and a rectum which terminates in the (usually) bilabiate anus.

The prestomach is known only in Clavelinidae, having been reported in *Clavelina cylindrica*, *C. moluccensis*, *C. nigra* n.sp., and *Nephtheis fascicularis*.

The oesophagus is long (occuping most of the length of the long abdomen) in Pycnoclavellidae, Polycitoridae (with the exception of the new genus *Brevicollus*), and *Euherdmania*. In all other taxa the oesophagus is of moderate length and the stomach is more or less halfway down the abdomen rather than at its posterior end.

Berrill (1950) ambiguously referred to the cylindrical region immediately posterior to the stomach as the posterior stomach, here called duodenum. It is especially long in *Eudistoma*, but is absent in *Nephtheis*, *Euclavella* n.gen., *Sycozoa* and the Didemnidae (which have no divisions of the gut distal to the stomach).

The narrow mid-intestine (sometimes with a posterior stomach along its length) intervenes between the duodenum and the rectum. In certain *Distaplia*, *Hypsistozoa*, and *Neodistoma* n.gen. a distinct rectal valve is at the junction of the rectum and the mid-intestine. The posterior stomach is in the otherwise relatively narrow mid-intestine of *Pseudodiazona*, Clavelinidae (in the descending gut limb), *Pycnoclavella* (in the pole of the gut loop), Polycitoridae and Stomozoidae (in the descending limb), and *Sigillina*, *Hypodistoma*, *Polydistoma* n.gen. (in the descending limb). There is no posterior stomach in Cionidae, *Rhopalaea*, *Nephtheis*, *Euclavella* n.gen., *Distaplia*, *Hypsistozoa*, *Neodistoma* n.gen., *Sycozoa*, and Didemnidae.

The ascending and descending limbs of the gut loop in Aplousobranchia are not homologous with those of Phlebobranchia and Stolidobranchia. In the latter two orders (in which the gut is bent up alongside the pharynx) the oesophagus, stomach, and proximal part of the intestine comprise the ascending limb. The intestine curves around in the pole of the loop and the descending limb consists of the distal part of the intestine and the rectum.

heart: In Aplousobranchia the heart is a straight, curved or V-shaped tube usually at the posterior end of the body. It is at the posterior end of the abdomen in taxa dealt with below. In Euherdmaniinae it is sometimes present halfway down the posterior abdomen, and in Polyclininae it is at the posterior end of the posterior abdomen (see Berrill 1936).

incubation of embryos: All Aplousobranchia except Cionidae and Diazonidae are viviparous, brooding embryos and releasing tailed larvae. In Clavelinidae the ovaries are relatively large, producing up to 100 eggs at a time. These are fertilised and are brooded in the distal end of the oviduct which, in some species, lies horizontally across the posterior end of the relatively roomy atrial cavity (see *Clavelina robusta* n.sp). The larvae complete their development free in the atrial cavity. In a few species (e.g. *C. moluccensis*) there is a pouch at the distal end of the oviduct in which the embryos are fertilised and brooded. In Pycnoclavellidae, which have a long oesophageal neck and generally smaller zooids and smaller ovaries than those of Clavelinidae, the eggs mature sequentially. They are fertilised at the base of the oviduct, and develop as they move up the long neck of the zooid toward the atrial cavity. Eggs are also fertilised at the base of the oviduct and develop as they move up the oesophageal neck in *Polycitorella* and *Cystodytes*, completing their development in a brood pouch at the top of the abdomen.

Berrill (1935a) believed that fertilisation at the base of the oviduct was characteristic also of *Polycitor* and *Eudistoma*. However, this is the exception rather than the rule in these diverse genera. Fertilisation is as the base of the oviduct in the Arctic *Polycitor vitreus* Sars (see Berrill 1948a) and in *Eudistoma olivaceum* (see Berrill 1947b). Of the 14 species of *Eudistoma* documented by Van Name (1945), only *E. clarum* appears to have eggs fertilised at the proximal end of the oviduct (see Van Name 1945, fig. 57). Most of the other species have eggs and embryos at different stages of development crowded in the atrial cavity where fertilisation probably takes place. Similarly, in the Australian species of these genera, fertilisation usually is in the atrial cavity, and is in the oviduct only in *Polycitor circes* and *P. annulus* n.sp. In *Eudistoma* only few eggs are produced and they are fertilised and brooded in the atrial cavity of the small, but numerous zooids. In zooids with the larval trunk about 1mm long, only one or two embryos are brooded at a time. Up to 8 embryos are found in the atrial cavity of each zooid in those species with particularly small larvae, in which the trunk is not more than 0.5mm (e.g. *Eudistoma elongatum*, *E. laysani*). Thus in *Eudistoma* the number of eggs produced and embryos brooded by each zooid is relatively low, and is directly related to the size of the zooids, and inversely related to the size of the larvae. In colonies in which the rate of replication is fast the large number of zooids producing eggs may well compensate for the small number that each zooid produces.

In Holozoidae a brood pouch is partially isolated from the zooid, allowing the embryo to incubate in the test independently of the zooid. A long incubation time is thus possible without restricting the functions of the zooid. Further, in some genera (*Distaplia* and *Sycozoa*) the larva escapes from the disintegrating test rather then being expelled through the atrial aperture. Therefore the necessity for eggs and embryos to remain small is removed. In this family ovaries produce few, but large eggs, embryos and larvae — some of the largest larvae known in the Ascidiacea (up to 4mm in *Sigillina*); and in the larvae of *Distaplia* and *Sycozoa* the adult organs are better developed than in any other taxon. Replication is also rapid and the large numbers of zooids in each colony all produce eggs. Thus the embryos produced by a holozoid colony are large, numerous, can be brooded for a long time, and the adult organs of the oozooid (primary zooid) and sometimes also blastozooids are well advanced before release of the larvae. These large larvae do not swim freely for very long, and their chances of recruitment far away from the parent colony appear minimal, unless the colony itself is uprooted and moved around in the plankton (as it is in *Sycozoa* spp.).

In some species (*Sigillina grandissima*, *Hypodistoma vastum* and *Distaplia retinaculata*) there are abnormally large eggs which rupture from the abdomen following fertilisation presumably at the base of the oviduct, and the embryos incubate free in the test as they do in all genera of Didemnidae. However, in Polyclininae eggs are fertilised and embryos incubate in the atrial cavity. In Euherdmaniinae, a variety of strategies for fertilisation and incubation of embryos reflect the polyphyletic nature of this subfamily. In *Euherdmania* (like *Pycnoclavella*) fertilisation is at the base of the oviduct and embryos incubate as they pass up the long oesophageal neck; in *Pseudodistoma* (like *Sigillina*) a brood pouch is attached to the posterodorsal corner of the thorax; and in *Ritterella* fertilisation is in the atrial cavity (as in Polyclininae).

incurrent aperture: see **apertures**.

internal longitudinal vessels: vessels on the inner surface of the pharyngeal wall, running parallel to its long axis. These vessels run over or between the stigmata. They are present in all phlebobranch and stolidobranch ascidians, and in *Ciona*, and Diazonidae. Vestiges of the papillae that support these vessels persist in the branchial sac of some genera of Euherdmaniinae (e.g. *Protopolyclinum* Millar, 1960) and *Polyclinum* (see **branchial papillae**).

larvae: All aplousobranch ascidians except *Ciona* and the Diazonidae are viviparous. Larvae are liberated from the adult zooids or colony with fully developed larval organs (tail, cerebral vesicle, and adhesive organs) and at least partially developed adult organs (branchial and atrial apertures, branchial sac and gut loop).

Larval ectoderm is particularly specialized, with secretory functions associated with larval settlement and the synthesis of test. Cloney (1977) has investigated the fine structure of larval adhesive organs, and has demonstrated (in *Distaplia occidentalis*) fine extensions projecting from the ectodermal cells into the test to anchor it against the ectoderm, and to carry secretions to the surface. Similar extensions of larval ectoderm from other parts of the larval trunk have been observed in many taxa during the course of the this study *viz.* in *Sycozoa* (*S. brevicauda* n.sp., *S. pulchra*), *Sigillina* (*S. grandissima* n.sp.), *Polycitor* (*P. translucidus*), *Eudistoma* (angolanum group, and *E. incubitum* n.sp.) and in *Brevicollus* n.gen. These extensions have terminal vesicles that often are conspicuous in the surface test and obscure the structure of the larvae. Other ectodermal projections into the test have been observed around the apertures of the oozooid in *Eudistoma carnosum* n.sp., *E. ovatum* and *E. purpureum* n.sp. The larval rastrum (see Kott 1980, 1982a) of certain *Diplosoma*, in which *Prochloron* symbionts are transferred from the parental cloacal cavity to the next generation, may be formed by similar ectodermal extensions over the posterior end of the haemocoel. The fine structure and the functions of these extensions deserve investigation.

There are basically 5 different types of larvae, each with characteristic adhesive organs (see above), known in the Aplousobranchia. Generally each is characteristic of a taxon or a group of taxa. However, often there are anomalous species with larvae that do not conform, and the phylogenetic significance of the differences between these larvae is not yet understood.

The known larval types are:

1. The small, undifferentiated larvae of *Ciona* and the Diazonidae develop from externally fertilised eggs. They have 3 sessile triradially arranged adhesive organs at the anterior end of the larval trunk. Adult organs remain relatively undifferentiated until settlement and metamorphosis. The larva is invariably small, its trunk being about 0.1mm long (see Berrill 1950).
2. The moderately large, well developed larvae of Clavelinidae, *Distaplia*, *Hypsistozoa*, *Sycozoa* and Stomozoidae are all relatively similar. They have 3 triradially arranged sessile or stalked, adhesive organs on a common stalk or plate that is connected to the developing oozooid only by a ventral stolon. The frontal plate (in Clavelinidae) and the stalks of the adhesive organs (in *Distaplia* and *Hypsistozoa*) are often expanded into rounded swellings (ampullae).

   Despite these similarities, differences exist in larvae as in adults, and a close phylogenetic relationship is not proposed between Clavelinidae and Holozoidae.

   The smaller larvae known in this group are in the Clavelinidae with a trunk that is 0.7mm long (*Clavelina australis*, *C. fecunda*), but more often they are 1mm or more. There are only 2 rows of stigmata in many of the species (*C. australis*, *C. fecunda*, *C. moluccensis* and *C. baudinensis*) while others have 4 rows (*C. meridionalis*, *C. oliva* n.sp. and *C. robusta* n.sp.) or more (*C. pseudobaudinensis*). Larvae have many fewer stigmata per row than the adult zooid and the gut loop is seldom differentiated.

   Larvae of *Distaplia* and *Hypsistozoa* have a larval trunk seldom less than 1.5mm long and often more than 2.0mm, and they have better developed adult organs than those of *Clavelina*. The adult complement of 4 rows of stigmata is present, the gut loop is well formed and blastozooids are present in many species.

   Sycozoa larvae are simplified, with trunks only about 1mm long, no ampullary expansions from the stalks of the adhesive organs, no ocellus, and although the epicardial sacs are often very conspicuous, without as many blastozooids as *Distaplia* and *Hypsistozoa*. However, the adult organs in the oozooid are as well developed as those in *Distaplia* and the axial cone in the adhesive organs is large.

   Larvae of *Clavelina dagysa* and *C. brasiliensis* (Millar, 1977) are unusual having apparently lost their adhesive organs, although they retain the frontal plate. The small (0.5mm trunk) larva of *C. baudinensis* is also unusual, lacking a stalked, frontal plate and a collar, or saucer of cells around the short-stalked adhesive organs. This may be a primitive condition, in which simple adhesive organs resembling those of oviparous forms are present, although they project on short straight stalks rather than being sessile. They do not have ampullary swellings found in other clavelinid larvae.

3. The relatively small larvae of *Polycitor* and *Eudistoma* (Polycitoridae), and most species of the Polyclinidae, have a larval trunk not more than 1mm long and stalked adhesive organs present in the mid-vertical line anteriorly. Conical, sometimes bilobed ectodermal ampullae are present in the anterior mid-line alternating with the adhesive organs, and/or in one or more rows along each side of them (especially in *Eudistoma* spp.). Polyclinidae have epidermal vesicles in the larval test as well as the ampullae. Adult organs are moderately well advanced in the larvae, although not as well as in the larger larvae of *Distaplia*, *Sycozoa* and *Hypsistozoa*. There are usually 2, but occasionally (in certain *Eudistoma*) 3, rows of stigmata.

   Didemnidae and *Cystodytes* (Polycitoridae) also have larvae of this general type, although their adhesive organs have conical protrusions rather than the flat-topped ones of *Polycitor* and *Eudistoma*.

   Polycitor annulus n.sp. and *P. circes* do not have the same larvae as other species in the genus. Instead they have triradially arranged adhesive organs. They resemble larvae of *Clavelina baudinensis*, and possibly reflect the common ancestry of aplousobranch ascidians from a prediazonid ancestor.

   Cystodytes has a circular perforated fold of test surrounding the stalked adhesive organs. It may have evolved from the polycitorid larval type.

4. The genera *Sigillina* and *Hypodistoma* contain the largest larvae known in the Ascidiacea (up to 4mm long larval trunk). They have 2 or 3 unusually large adhesive organs in the anterior mid-line. Adhesive organs are sessile, on a frontal plate connected to the oozooid by a ventral stolon in *Hypodistoma*. In *Sigillina* the anterior end of the larval trunk (which contains the larval adhesive organs) is separated from the oozooid by a waist. Adhesive organs are on short thick stalks and surrounded by ectodermal vesicles that arise from the ectoderm around the base of these stalks, just in front of the waist. Adult organs in these large larvae are not well differentiated. The 3 rows of stigmata are present, but the gut loop usually cannot be distinguished. These larvae have short tails and could be poor swimmers, probably causing population isolation, resulting in relatively numerous species in this southern hemisphere group of genera.

   The large larva of *Sigillina mjöbergi*, with 2 deeply invaginated tubular adhesive organs (like those of Pycnoclavellidae), is anomalous, suggesting *Sigillina*, as presently defined, is polyphyletic.

5. Larvae with adhesive cells in the base of deeply invaginated, tubular adhesive organs which evert on settlement occur in Pycnoclavellidae, *Euherdmania* and *Sigillina mjöbergi*. These larvae are moderate to large (0.7 to 2.0mm long trunk). They have 3 (triradially arranged) or 2 (in the anterior vertical mid-line) adhesive organs. Sometimes there are deep longitudinal furrows in the ectoderm around the anterior half of the trunk (ampullae: Trason 1957) and often the otolith is absent. The oozooid is not always well advanced before settlement, usually the gut loop is not differentiated and only one or 2 rows of stigmata can be seen. Exceptions are *Pycnoclavella detorta* with 6 rows of stigmata and *Euclavella* n.gen. *claviformis* with 4 rows. Both have 3 adhesive organs, a well differentiated gut loop, and neither have an otolith.

   These larvae have no obvious morphological affinity with any of the other groups except the primitive cionid-diazonid larvae. They may indicate an origin from forms with a sessile group of adhesive cells which subsequently invaginated into the larval haemocoel. The larvae may indicate a relationship between Pycnoclavellidae and Euherdmaniinae, and they are evidence of the polyphyletic nature of the latter sub-family.

In all incubating aplousobranch larvae the tail winds around the mid-line. As it extends up the anterior face of the trunk and (if long enough) back along its upper surface, it passes to the right of the adhesive organs (if these are in a vertical line) and the sensory vesicle. If adhesive organs are triradially arranged 2 are on the left and one is on the right of the tail. (See also **adhesive organs**).

neural complex, — ganglion, — gland: a closely associated neural ganglion and gland beneath the epidermis in the intersiphonal region. In the Aplousobranchia (as in the other enterogonid suborder, Phlebobranchia) the sometimes flask-shaped neural gland is ventral to the ganglion, and its duct opens directly into the pharynx in the mid-dorsal line at the anterior end of the dorsal lamina. In most Aplousobranchia the opening of the neural gland is a small, inconspicuous, sessile, simple vertical or horizontal slit, or pit. *Ciona* is the exception, the opening of the gland (the ciliated pit) being complex and folded, and opening on a tubercle as it does in phlebobranch and stolidobranch ascidians (see Millar 1953a).

oviparous: externally fertilised (see also **viviparous**).

proximal: the end of an organ or structure away from which the contents or products move. (See also **distal**).

pyloric gland: see **gastro-intestinal gland**.

rectal valve: two backward-projecting caecae at the proximal end of the rectum, found in certain *Distaplia* and in *Hypsistozoa* and *Neodistoma* n.gen.

replication: the vegetative process whereby clones of adult zooids are produced to form colonies. One or another process of replication occurs in all aplousobranch families except the Cionidae (see also **cloacal systems, colonies, epicardial sacs**; and Berrill 1935b, Kott 1982b).

retropharyngeal groove: the groove that connects the postero-ventral end of the endostyle with the postero-dorsal oesophageal opening.

spicules: small (0.01 to 0.1mm diameter), calcareous (calcite) crystalline structures found in Didemnidae and in *Polycitorella* and *Cystodytes*. They appear to be synthesised in localised regions of the test where it is in close contact with the zooid epidermis on each side of the ventral mid-line. The site of spicule formation in Didemnidae is well documented (Lafargue and Kniprath 1978) but that in *Cystodytes* and *Polycitorella* is less certain. Spicules are plate like (*Cystodytes*), star-shaped (Didemnidae, *Polycitorella*), or spherical (Didemnidae, *Polycitorella*).

vegetative stolon: see **epicardium**.

Suborder APLOUSOBRANCHIA Lahille, 1887

The suborder contains families of the Ascidiacea in which the body is divided into the thorax (containing neural apparatus, branchial and atrial apertures and pharynx surrounded by the atrial cavity) and the abdomen (containing gut loop, heart and gonads). The epicardial sacs, developed in the embryo as outgrowths from the posterior end of the pharynx, have a regenerative function. They persist as sacs or remnants of sacs in the adult abdomen and sometimes extend into a posterior abdominal extension. Most species of the Aplousobranchia are colonial. With the exception only of the Clavelinidae, the endodermal epicardial sacs are the tissue from which all body organs of replicated zooids develop following horizontal division of the zooid at one or more levels posterior to the thorax (Berrill 1935b). In *Ciona* and in most *Rhopalaea* the generative role of the epicardial epithelium is confined to the repair of parts of the body following loss or damage, for in these solitary taxa vegetative replication does not occur.

In Clavelinidae replicated zooids develop from isolated terminal ampullae of test vessels in the colony stalk (see Berrill 1950). In the few *Clavelina* that are solitary, replicates either are separated from one another following their formation (as in *Clavelina miniata* Watanabe and Tokioka, 1973 and possibly *C. oliva* n.sp.), or they develop following resorption of the parent zooid, as in *Clavelina ostrearium* (Michaelsen, 1930) and *Clavelina meridionalis* (Herdman, 1899).

As discussed for colonial species of the Stolidobranchia (Kott 1985), zooids decrease in size as the replicative process evolves and becomes more prolific, and colonies become more highly organised. Most families of Aplousobranchia have relatively few, large, yolky viviparous larvae. These are incubated either in the zooids, or in brood pouches, or free in the test. Exceptions are *Ciona* and Diazonidae, in which fertilisation is external, and numerous small larvae with poorly organised larval organs are produced. The size of the larva, the evolutionary history of the species, and its degree of colonial organisation are all directly related to one another and inversely related to the numbers of embryos produced and incubated (see Berrill 1935a, 1955; Kott 1974, 1982b, 1985).

The most fundamental plesiomorphic character in the Aplousobranchia is possibly the capacity for replication. As indicated, the process is not the same in all families, and aspects of the various processes are often useful indicators of phylogeny. Thus, although in Clavelinidae, Pycnoclavellidae and Holozoidae a well developed vascular stolon from the posterior end of the abdomen is involved with replication, the process is different in each family. Replication in Clavelinidae is from the terminal ampullae of the vascular process, in Holozoidae it is by division of the stolon, and in Pycnoclavellidae the abdomen itself is divided. In Polycitoridae and Diazonidae the process is the same — the abdomen divides to form the replicates. This suggests the two families are related. Kott (1982b) has summarised the range of different replicative processes known in the Aplousobranchia. Despite differences in the process, morphological adaptations associated with increasingly prolific replication of any type are usually convergent, *viz.* size and simplification of the zooids, size and form of the colony, and its degree of organisation and capacity to brood viviparous embryos.

Other possibly plesiomorphic characters, probably not convergent, that could be indicative of common ancestry, are the larval adhesive organs. The everting cones of the majority of taxa (Clavelinidae, Holozoidae, Polycitoridae, Polyclinidae, Didemnidae) can be traced to the primitive, simple, non-everting, sessile, conical type found in the small larvae of all oviparous ascidians (phlebobranch and stolidobranch taxa as well as *Ciona* and the Diazonidae). However, deep tubular invaginations that carry the secretory cells back into the larval trunk, in Pycnoclavellidae, *Sigillina mjöbergi* and *Euherdmania* (Euherdmaniinae), do not have obvious relationships with the other types of adhesive organs (see Cloney 1977; see also Annotated Glossary, **adhesive organs**).

Characters associated with the progressive evolution of cloacal systems are often convergent and usually indicative of not more than generic status — only rarely are families so distinguished (*viz.* Euherdmaniinae from Polyclininae). Thus, in the Holozoidae, *Sigillina* (with atrial apertures on siphons opening independently) is distinct from *Sycozoa* and *Distaplia* which have cloacal cavities and wide atrial apertures opening into them. Differences in the arrangement of zooids in the colony, either in cloacal systems or with atrial siphons opening separately to the exterior, are usually regarded as significant only at species level. Thus in some, but not all, *Eudistoma* zooids are arranged in circles around rudimentary cloacal cavities; and *Distaplia* has either circular or radiating double row, systems.

Reduction in gonad size is another convergent character associated with replication, a colonial habit and viviparity (see Kott 1982b). However, the location of gonads in the zooid is only sometimes convergent. Polycitoridae have small zooids with gonads in the abdomen (in the gut loop). Similarly, neither Holozoidae nor Didemnidae have a posterior abdomen and their gonads are also in the gut loop, in what appears to represent maintenance of their primitive position rather than convergence with the Polycitoridae. However, the presence of gonads in a posterior abdomen in certain genera of the Euherdmaniinae may be convergent, rather than indicative of a direct relationship with Polyclinidae — e.g. *Pseudodistoma* has an apparently closer phylogenetic relationship with *Sigillina* than with Polyclinidae (with which it currently is classified). The Euherdmaniinae will be discussed in Part 3 of this work.

Holozoidae and Didemnidae both produce relatively few and large eggs. Embryos are brooded in thoracic pouches in most species of the Holozoidae and in *Atriolum* Kott, 1983 (Didemnidae). A few species of Holozoidae have particularly large eggs which rupture directly from the abdomen to develop in the test as they do in most Didemnidae. These appear convergent characters associated with the relative size of eggs and zooids, for a direct phylogenetic relationship between Holozoidae and Didemnidae is denied by their processes of replication — the division of a posterior abdominal vegetative stolon in Holozoidae, and oesophageal budding and division of the zooid in Didemnidae.

Unlike Phlebobranchia and Stolidobranchia, where phylogenetic relationships can be identified with a degree of confidence, relationships between many recognised families of Aplousobranchia are obscure. Their morphology is diverse, presumably as a result of wide radiation. Subsequent extinctions have left gaps in the extant fauna and a shortage of evidence from which to deduce phylogeny. Further, several monotypic taxa have remarkably wide geographic ranges, but are known from only isolated records and localities (*viz. Pseudodiazona*, Stomozoidae n.fam., *Nephtheis* and *Euclavella* n.gen), suggesting that conditions favouring radiation in these groups are not as favourable now as they were in the past, and that the present populations are relict ones.

The Aplousobranchia is not well represented in the abyssal fauna of any ocean. Possibly its characters are not readily adapted to conditions in ocean depths. One relevant character may be the large, viviparous larvae (associated with a colonial habit) that are free for only very short periods, and are unlikely to be efficient swimmers. These inhibit gene flow between populations isolated by distance or other factors. The internal fertilisation that is necessarily associated with a viviparous habit may also represent a selective disadvantage at great depths where conditions on the sea floor apparently accommodate only sparse populations. These reproductive strategies may reflect selective pressures that have affected evolution of aplousobranch ascidians and patterns of distribution of extant forms.

Only few of the known genera of Aplousobranchia are not known from Australian waters.

KEY TO THE FAMILIES OF THE APLOUSOBRANCHIA

1. Internal longitudinal branchial vessels or forked papillae present 2
   Internal longitudinal branchial vessels and forked papillae absent 3
2. Gut forms a horizontal loop ....CIONIDAE
   Gut forms a vertical loop ....DIAZONIDAE
3. Branchial apertures with smooth borders ...4
   Branchial apertures with lobed borders 5
4. Ovary contains < 10 ova; larval adhesive organs inverted tubes ...PYCNOCLAVELLIDAE new family
   Ovary contains > 10 ova; larval adhesive organs not inverted tubes ......CLAVELINIDAE
5. Gonads and heart in a posterior abdomen ............POLYCLINIDAE
   Gonads and heart not in a posterior abdomen 6
6. Lobes of apertures with secondary serrations ....STOMOZOIDAE new family
   Lobes of apertures without secondary serrations 7
7. Replicates generated from vegetative stolon in stalk or in base of colony; embryos usually brooded in thoracic pouch; calcareous spicules never present ....HOLOZOIDAE
   Replicates not generated from vegetative stolon in stalk or in base of colony; embryos seldom brooded in thoracic pouch; calcareous spicules sometimes present 8
8. Cloacal systems seldom present*; atrial apertures always 6-lobed; replication by horizontal division of the abdomen ............POLYCITORIDAE
   Cloacal systems always present, atrial apertures seldom 6-lobed; replication by oesophageal budding ....DIDEMNIDAE

* The new genus *Exostoma* is the only taxon of the Polycitoridae with a true cloacal system.

Family CIONIDAE Lahille, 1887

Ciona, the only known genus of this family, is characterised by its solitary habit, horizontal gut loop posterior to the thorax, persistent openings of the epicardial sacs into the pharynx, lobed apertures, and large branchial sac with numerous rows of stigmata and internal longitudinal vessels supported on papillae which project into the lumen. What are thought to be light sensitive ocelli are present between the lobes of the apertures.

Kott (1969) first drew attention to the aplousobranch nature of the Cionidae, which formerly had been included (with the Diazonidae) in the Phlebobranchia on the basis of the internal longitudinal branchial vessels and their supporting papillae which are similar to those of certain phlebobranch ascidians (see Huus 1937 Van Name 1945, Berrill 1950). A tendency to lose internal longitudinal branchial vessels is a convergent adaptation associated with the development of vegetative replication and consequent reduction in zooid size in both phlebobranch and stolidobranch as well as in aplousobranch ascidians (Kott 1985). Consequently, the absence of these vessels from the small branchial sacs of colonial aplousobranchs is a secondary adaptation, and not a plesiomorphic character indicating a phylogenetic affinity at the subordinal level.

As well as its large branchial sac and internal longitudinal branchial vessels, *Ciona* has other apparently primitive characters that persist in solitary Phlebobranchia and Stolidobranchia viz. small larvae and an oviparous habit. In all sub-orders, convergent adaptations associated with vegetative replication and a colonial habit include viviparity and the development of large, well organised larvae with well developed larval and adult organs (see Kott 1985). Thus, small, largely undifferentiated cionid-type larvae, with simple triradially arranged adhesive organs, do not indicate a close phylogenetic relationship between *Ciona* and solitary phlebobranch ascidians. They are associated with a solitary, oviparous habit and their loss represents another adaptation associated with the colonial habit that results from vegetative replication.

The hypothesis of a closer relationship between *Ciona* and Aplousobranchia is more compelling than one between *Ciona* and Phlebobranchia. It is based on the existence and regenerative role of the epicardial sacs in *Ciona* and in aplousobranch families. Individuals of *Ciona intestinalis* have the capacity to regenerate lost organs, the regenerative tissue being endodermal epicardium. Epicardial epithelium is the regenerative tissue in the process of replication in most aplousobranch ascidians (Hirschler 1914, Berrill 1935b). Although regeneration and repair occur in *Ciona*, spontaneous division of the zooid resulting in replication does not. The regenerative capacity of the epicardial tissue in *Ciona* involving selection of epicardial tissue for a regenerative function, rather than the excretory role it has assumed in Phlebobranchia, probably represents an early stage in the evolution of the aplousobranch vegetative process, and the separation of Aplousobranchia from Phlebobranchia.

The close relationship between *Ciona* and other aplousobranch ascidians is supported by the oxidation state of the vanadium present in the blood cells, vanadium (IV) in aplousobranch and vanadium (III) in phlebobranch families (Hawkins, Kott, Parry and Swinehart 1983).

Test vessels of *Ciona* arise from the posterior end of the body and extend out into the posterior test extensions (villi). Although these vessels are primarily ectodermal, as in all ascidian species, they have a mesenchymal septum between the two channels (see Millar 1953a), as in the aplousobranch family Clavelinidae and provide a further indication of affinity with Aplousobranchia.

Araneum Monniot and Monniot, 1973, assigned by its authors to the family Cionidae has no apparent cionid characters. It appears a highly adapted, abyssal phlebobranch related to the Ascidiidae.

Genus **Ciona** Linnaeus, 1767

Type species: *Ascidia intestinalis* Linnaeus, 1767

A very soft test in combination with strong, external longitudinal muscle bands that extend the whole length of the organism, make *Ciona* particularly contractile. There is also an inner layer of fine circular muscles. The branchial aperture is usually 8-lobed and the atrial aperture 6-lobed, both with single, probably light sensitive, ocelli (see Millar 1953a) between the lobes.

Hoshino and Nishikawa (1985) have exhaustively reviewed *Ciona*. They have examined many of the available specimens that have formerly been described, as well as additional material from Arctic, boreal and cold and warm temperate European waters, the Mediterranean, the Atlantic coast of North and South America, the coast of California and Japanese waters as well as some specimens from Western Australia, Port Jackson and New Zealand. They conclude there are two closely related species of the genus — one, *Ciona intestinalis* (Linnaeus), with a wide cosmopolitan range, as indicated below, and one, *Ciona savignyi* Herdman, recorded principally from Japan, but also recorded from Alaska (as *C. intestinalis*: Ritter, 1913) and Hong Kong (*C. intestinalis*: Kott and Goodbody, 1982, part). A further record from Argentina (Pisano, Rengel and Bustuoabad 1971), assigned to *C. savignyi* on biological grounds, is difficult to interpret in view of the otherwise limited range of the species from Japan to the northern Pacific. *Ciona intestinalis* is the only species recorded from Australia.

Two further species are possibly valid, *viz.* the southern polar *C. antarctica* Hartmeyer, 1911 (see Monniot and Monniot 1983) which has a distinctive flattened, leaf-like ovary (see Hoshino and Nishikawa 1985), and the north-eastern Atlantic abyssal *C. imperfecta* Monniot and Monniot, 1977. Two possibly valid subspecies, *C. intestinalis longissima* Hartmeyer, 1899 and *C. intestinalis gelatinosa* Bonnevie, 1896, both with a posterior abdominal vascular extension, have been described from Arctic waters (see Hoshino and Nishikawa 1985).

Ciona intestinalis (Linnaeus, 1767)
(Fig. 3, Plate 1a)

Tethyum sociabile Gunnerus, 1765, p. 99.
Ciona sociabilis: Hartmeyer, 1915a, p.321; 1915b, p.254.
Ascidia intestinalis Linnaeus, 1767, p.1087. Cuvier, 1815, p.32. Couthouy, 1838, p.111. Dekay, 1843, p.259. Sars, 1851, p.156; 1859, p.64.
Phallusia intestinalis: Savigny, 1816, p.107.
Ciona intestinalis: ? Fleming, 1822, p.512. Kuppler, 1875, p.207. Heller 1875, p.117. Schmeltz, 1879, p.89. Traustedt, 1882, p.454. Roule, 1884, p.7. Castle, 1896, pls 1-13. Damas, 1899, p.1. Herdman, 1899, p.9. Hartmeyer, 1903, p.297; 1915a, p.321; 1920, p.210; 1924, f. typica p.90, f. tenella p.103, f. ocellata p.104. Alder and Hancock, 1907, p.37. Kesteven, 1909, f. sydneiensis p.282. Van Name, 1912, f. tenella p.606; 1945, f. tenella p.163.? Huntsman, 1912a, p.108; 1912b, pp.112, 114, 119. Sumner, Osburn and Cole, 1913, p.730. Pratt, 1916, p.667. Ritter and Forsyth, 1917, p.457. Hartmeyer and Michaelsen, 1928, p.259. Arnback, 1934, var. tenella p.17. Brewin, 1950, p.347. Millar, 1953a, p.1; 1963a, p.720; 1970, f. costata p.114. Kott, 1952, p.319; 1976, p.54. Kott and Goodbody, 1982, p.505 (part, QM G12780). Hoshino and Nishikawa, 1985, p.63.
Ascidia canina Mueller, 1776, p.225.
Ciona canina: Kuppler, 1875, p.206. Traustedt, 1880, p.432.
Ascidia ocellata Agassiz, 1850, p.159. Binney, 1870, p.24. Dall, 1870, p.255.
Ciona ocellata: Verrill, 1880 p.251. McDonald, 1889, p.858. Hartmeyer, 1903, p.301.
Ascidia tenella Stimpson, 1852, p.228; 1854, p.20; 1860, p.2. Binney, 1870, p.24. ? Dall, 1870, p.255.
Ciona tenella: Verrill, 1871, p.99; 1872a, p.6; 1872b, p.214; 1873, vol.6 pp. 435, 440; 1874, vol.7 pp. 413, 504; 1880, p.25. Verrill and Smith, 1873, p.698. Kingsley, 1901, p.183. Whiteaves, 1901, p.267. Hartmeyer, 1903, p.301.
Ascidia pulchella Alder, 1863, p.157.
Ciona indica Sluiter, 1904, p. 24 (part, specimen from Station 312).

Ciona pulchella: Alder and Hancock, 1907, p.14. Hartmeyer, 1915a, p.321.

Ciona fascicularis Hancock, 1870, p.364. Kuppfer, 1875, p.207. Alder and Hancock, 1907, p.15. Hartmeyer, 1915a, p.321.

Ciona diaphanaea Kesteven, 1909, pp.282, 285.

Ciona robusta Hoshino and Tokioka, 1967, p.275.

Ciona gelatinosa: Monniot, C., 1969b, p.1133.

DISTRIBUTION

NEW RECORDS: Western Australia (Albany town jetty, WAM 744.83). South Australia (Adelaide outer harbour, SAM E1978-9). Victoria (Portland Harbour, QM GH34; Port Melbourne, QM G10048).

PREVIOUSLY RECORDED: Western Australia (Canning River, Swan River — Hartmeyer and Michaelsen 1928; Fremantle, Albany — Hartmeyer and Michaelsen 1928, Kott 1952). South Australia (Port Adelaide — Kott 1952). Tasmania (Hobart — Kott 1952). Victoria (Port Phillip Bay — Kott 1976). New South Wales (Port Jackson — Herdman 1899, Kott 1952). Queensland (Rockhampton — Kott 1952). Indonesia (ZMA TU333 specimen from St. 312 Sluiter 1904).

Re-examination of Hong Kong material in the Queensland Museum (see Kott and Goodbody 1982) shows the species on the hull of the Fisheries Vessel (M62) to be *C. intestinalis* (QMG12780). All other specimen lots, both from inside Tolo Harbour and in the South China Sea, are *C. savignyi*.

Ciona intestinalis is known also from the Arctic, the east Atlantic part of the boreal region, around the British coasts, the western seaboard of Europe, the Mediterranean, parts of north and south America, Cape Verde, and New Zealand (Brewin 1950, Millar 1953a). Van Name (1945 p.162) summarises the American records as 'from Greenland and Davis Strait south to southern Massachusetts and Rhode Island and on the Pacific coast from southern Alaska to the southern end of California'.

However, the only confirmed records on the Pacific coast of north America (see Hoshino and Nishikawa 1985) are from California. As *C. savignyi* has a known range that includes the Pacific coasts of Alaska and Canada, it is possible that records of Dall (1870) and Huntsman (1812a, b) are of *C. savignyi* rather than *C. intestinalis*.

The Australian records are all from harbours and port installations, and several (Hartmeyer and Michaelsen 1928) are from brackish locations well up river estuaries. However, the most recent records are not less than 10 years old. The species appears to be disappearing from Australian harbours, where, from 1950 to 1960, crowded populations were known to occur. Van Name (1945) observed the same phenomenon on the northern coast of New England where *Ciona* disappeared almost completely from a region where it had been common in the mid-19th century. The species is flourishing in Hong Kong and is especially common in the same

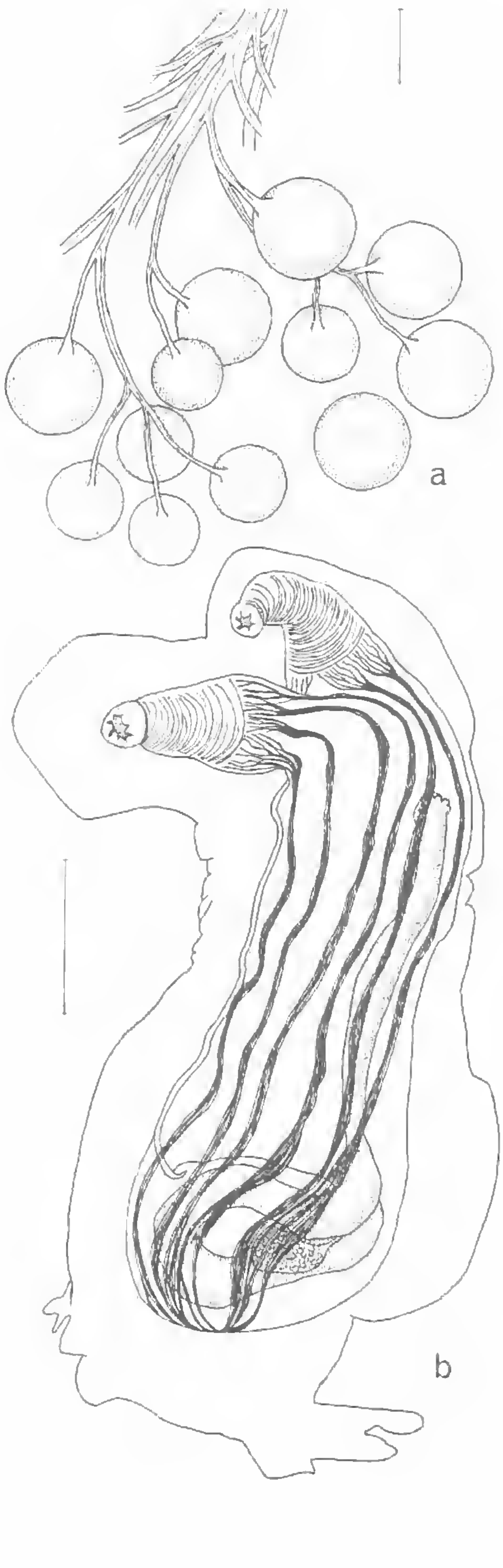


FIG. 3. *Ciona intestinalis* (QM GH34): **a**, terminal ampullae: **b**, individual in test showing gut-loop and muscles. Scales. **a**, 1mm: **b**, 5mm.

habitats (on ships hulls, wharf piles etc) as it used to occupy in Australia (Kott and Goodbody 1982).

It is possible that *C. intestinalis* is adapted for a habitat on under surfaces such as ships hulls — an adaptation that would favour its transport and cosmopolitan distribution on ships — a proposal first made by Van Name (1945). This proposal was repeated by Kott (1969, 1974). Kott (1974) suggested that populations were confined to ports and harbours because there they could be maintained in sufficient densities for successful sexual reproduction; while in the conditions outside these protected locations larvae would be dispersed and ultimately reach sexual maturity in isolation from other individuals of the species.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are always found crowded together in large populations. They are cylindrical, up to 15cm long when extended, and usually hang vertically from under surfaces, fixed by their posterior ends. The siphons are of variable length, the 8-lobed branchial siphon terminal and the 6-lobed atrial antero-dorsal. The test is soft and translucent. When the animal is contracted it is very wrinkled on the surface, but internally the soft gelatinous mass becomes thicker. Occasionally tubicolous worms and other epibionts are attached sparsely to the outer surface and the outer layer of test is sometimes quite hard and leathery.

The single, possibly light sensitive, ocellus between the lobes of the apertures each consists of a central red spot surrounded by a patch of orange pigment. Posteriorly the test is produced into short projections (villi), that help to anchor the animal, and that contain the double-channelled test vessels with large (1.5mm diameter) spherical terminal ampullae.

INTERNAL STRUCTURE: The most conspicuous feature of the body wall is the long parallel muscle bands, 6 on each side, 4 of which extend from the branchial siphon to the posterior end of the body; and 2 from the atrial siphon to the same point at the posterior end of the body. There also is a pair of fine ventral muscles along each side of the endostyle. Anteriorly the longitudinal muscles extend along the siphons beneath circular siphonal muscles. A layer of circular muscle fibres is present beneath the longitudinal muscles. From 60 to 100 simple branchial tentacles (the number increasing with the size of the individual) encircle the siphon base. Larger tentacles, of 3 orders of size, alternate with rudimentary ones. The dorsal tubercle, in a shallow prebranchial area, has a simple U-shaped slit, with the horns turned out. In larger specimens the slit becomes convoluted and complex, with some side branches. A row of pointed, tentacle-like, antero-posteriorly flattened dorsal languets, each expanding from a transverse vessels where it crosses the dorsal sinus, extends the whole length of the branchial sac, and curves to the right of the conspicuous oesophageal opening at the posterior end.

The endostyle also extends the whole length of the branchial sac and continues posteriorly into a curved and usually (but not always) pointed evagination from the postero-ventral corner of the branchial sac — the endostylar appendix. Two of the newly recorded specimens (QM GH34) have a short endostylar appendix, rounded at its tip. Occasionally, the appendix is turned up to the left of the branchial sac (QM G10048; see Roule 1884, pl.1 fig.5). The retropharyngeal groove extends across the posterior end of the pharynx from the base of this appendix to the oesophageal opening. The small paired openings to the epicardial sacs are close together in the retropharyngeal groove just dorsal to the base of the endostylar appendix.

The most conspicuous feature of the branchial sac are the internal longitudinal vessels, bearing spoon-shaped papillae that project into the pharynx at their junctions with the transverse and parastigmatic vessels. There are from 30 to 130 longitudinal vessels per side, increasing in number as the individual grows. Stigmata are long and narrow, and, like the longitudinal vessels, increase in number with the size of the individual, from 4 to 8 per mesh.

The gut loop is behind the pharynx — in an abdomen — although there is no constriction of the body wall separating it from the thorax. The oesophagus, from the postero-dorsal corner of the pharynx, curves postero-ventrally slightly to the right of the midline and opens into an almost spherical stomach that is more or less tapered at each end and lies in the dorsal curve of the posterior end of the body. The stomach has about 40 longitudinal ridges in its inner lining. From the distal end of the stomach, the intestine curves anteriorly and then dorsally to lie across the posterior end of the body to the left of the stomach. The rectum extends anteriorly, dorsal to the gonoducts, and opens about two-thirds of the distance up the branchial sac in a lobed anal aperture.

The gonads are also in the abdomen, the testis follicles being minute tubules connected by vasa efferentia, and forming a furry-looking coating over the stomach and intestine. The ovary, a simple sac becoming larger and less regular in older individuals, lies to the left of the stomach and just behind the horizontal limb of the intestine. Male and female ducts extend anteriorly inside the rectum. Both gonoducts extend anterior to the anus, however, to open at the base of the atrial siphon. The tip of the male duct is swollen into a small bulb that has in the vicinity of 20 separate minute tubular openings on its upper surface. There is usually a cap of red pigment over the terminal bulb that persists in alcohol preservative over many years.

REMARKS: *Ciona intestinalis* has an endostylar appendix with epicardial openings close to it, and the tip of the male gonoduct has a red pigment cap over it. *Ciona savignyi* lacks an endostylar appendix and has epicardial openings close to the oesophagus. Some *C. intestinalis* are distinguished further by the cuticular layer of the test acquiring a leathery consistency.

A distorted and mutilated specimen from Indonesia (Flores Sea ZMA TU333 *Siboga* station 312) assigned to *Ciona indica* Sluiter, 1904 is a specimen of *Ciona intestinalis*. The openings of the gonoducts are mutilated anterior to the anus, and their exact form and position could not be determined. However, the endostylar appendix is present in the position usual for *C. intestinalis* at the distal end of the endostyle; secondary branchial papillae, though small and often compressed, are also present (Sluiter 1904 pl.IV fig 2); and, as Nishikawa has reported (Hoshino and Nishikawa 1985) the muscles, gut, gonads, and epidicardial sacs and their openings are all characteristic of *C. intestinalis*. The flaccid and mutilated test of this sessile specimen was stuck onto the firm, gelatinous test of portion of a polycitorid colony, but it does not appear that the living specimen was so attached. Specimens of *Ciona indica* from *Siboga* station 49 (also from the Flores Sea) have been found to be conspecific with *Rhopalaea crassa* (see Hoshino and Nishikawa 1985).

Detailed accounts of the morphology and histology of *C. intestinalis* are given by Roule (1884) and Millar (1953a).

Family DIAZONIDAE Seeliger, 1906

Members of the family display primitive characters shared with the Cionidae, *viz.* numerous inner longitudinal branchial vessels, a large branchial sac, and a gelatinous, translucent test. It is the only other family of the Aplousobranchia that, like Cionidae, has large numbers of externally fertilized eggs, and larvae with sessile, triradially arranged adhesive organs each consisting of a group of specialized epidermal cells and a cerebral vesicle but little other organisation of trunk organs (Berrill 1950). Also like Cionidae, zooids have 6-lobed incurrent and excurrent apertures. The gut loop is vertical and posterior to the branchial sac and usually encloses the large gonads — although these are sometimes present in a posterior abdomen. Gonoducts open near the anus, well anterior near the base of the atrial siphon, as is usual for oviparous species (see Kott 1985). Body muscles are longitudinal, extending down the body from both siphons. No oblique muscles extend posteriorly from the endostyle as in Clavelinidae.

The family appears related phylogenetically to Cionidae, being separated from it by the extension of the gut into a vertical rather than horizontal loop, and by the progressive development of vegetative replication through simple strobilation of the abdomen involving the epicardial sac as the regenerative tissue (see Berrill 1935a, 1950 for *Diazona*). The mesodermal septum that develops in the vascular stolon of *Ciona intestinalis* is not present in Diazonidae.

Species range from solitary individuals (*Rhopalaea*) to colonies with completely embedded zooids (*Syndiazona*, *Pseudodiazona*). Vegetative replication, although it is not prolific, takes place in most species. In *Rhopalaea* a number of species are solitary but regeneration of the thorax is apparently a common occurrence. Progressive reduction in zooid size with the evolution of more prolific vegetative replication is well demonstrated in this family — the zooids of solitary *Rhopalaea* being much larger than those of colonial *Diazona* spp.

There is some variation in the course of longitudinal muscles. Generally they extend along the thorax and the abdomen. However, in *Rhopalaea crassa* they are confined to the thorax, and in *R. nordgaardi* they continue onto a vascular stolon. In both *Tylobranchion* and *Pseudodiazona* there is a true posterior abdomen with muscles extending onto it from the abdomen, and with gonads and heart in it that appear spilt over from their primitive position in the gut loop. These changes (possibly related to reduction in zooid size associated with increasing efficiency of vegetative replication as the colonial habit evolves), suggest a relationship with Polyclinidae, in which zooids, with gonads and heart in a posterior abdomen, have internal longitudinal branchial vessels reduced to simple papillae (*Ritterella* spp., *Protopolyclinum* and *Polyclinum*) or lost altogether.

Occasionally (in *Tylobranchion*) there are forked branchial papillae rather than continuous internal longitudinal vessels. However, the reduction of internal longitudinal vessels to forked papillae appears to be a genetic character indicating a taxonomic difference rather than an intraspecific variation as C. Monniot (1969a) suggested when he proposed the synonymy of *Rhopalaea nordgaardi* Hartmeyer, 1922 with *Tylobranchion* — a proposal earlier rejected by Ärnbäck (1927).

Rhopalaea and *Pseudodiazona* Millar, 1963a (monotypic) are the only Diazonidae represented in Australia. Others known are *Diazona* Savigny, 1816 (polytypic), *Syndiazona* Oka, 1926 (polytypic) from the Philippines, Japan and French Polynesia, and *Tylobranchion* Herdman, 1886 (monotypic) from the Antarctic (see Kott 1969). Even genera at present known polytypic are not diverse, *Diazona* has 3 species — 2 from the western Atlantic (see Van Name 1945) and the type *D. violacea* Savigny from Europe. *Rhopalaea* contains 7 species (see below) and *Syndiazona* has only 2 species from the western Pacific.

Syndiazona chinensis Tokioka, 1955 is known from the East China Sea (Tokioka 1955a), the Philippines (Millar 1975, and new records QM GH521 GH531), the Kei Is (Millar 1975), and French Polynesia (> *Rhopalaea piru* Monniot and Monniot, 1987; see below, *Rhopalaea*). Millar (1975) thought that *Polycitor renziwadai* Tokioka 1952 from the Arafura Sea also may be a specimen of this species. However, Tokioka did not observe a posterior abdomen or internal longitudinal vessels, and his specimen has fewer rows of stigmata than are found in *S. chinensis*. It therefore seems more likely that *P. renziwadai* is correctly assigned to the genus *Polycitor*. Nevertheless, despite the present absence of records, it is not unlikely that *S. chinensis* will be found to occur in Australian tropical waters as it already is known to range widely in the western tropical Pacific.

KEY TO THE GENERA OF DIAZONIDAE
(* not recorded from Australia)

1. Zooids solitary or at most 2 embedded in common test .... *Rhopalaea*
   Zooids numerous, never solitary, partially or completely embedded in common test.......2
2. Zooids partially embedded in common test... *Diazona**
   Zooids completely embedded in common test...3
3. Muscular extension containing gonads present posterior to the abdomen 4
   Muscular extension containing gonads not present posterior to the abdomen............... .... *Syndiazona**
4. Heart halfway down the posterior abdomen............................ *Tylobranchion**
   Heart at the posterior end of posterior abdomen .... *Pseudodiazona*

Genus **Rhopalaea** Philippi, 1843

Type species: *Rhopalaea neapolitana* Philippi, 1843

The genus is characterised by its large pharynx, with internal longitudinal branchial vessels and numerous rows of stigmata. The abdomen is separated from the thorax by a narrow oesophageal neck, and is tightly contained in firm abdominal test. Numerous longitudinal thoracic muscles sometimes extend onto the abdomen.

Five of the 7 known species of the genus *Rhopalaea* are solitary, *viz. R. abdominalis* (Sluiter, 1898), *R. birkelandi* Tokioka, 1971, *R. crassa* (Herdman, 1880), *R. tenuis* (Sluiter, 1904) and the type species *R. neapolitana. Rhopalaea nordgaardi* Hartmeyer, 1922 from Norway and *R. hartmeyeri* Salfi, 1927 from the Gulf of Naples are the only 2 species found as colonies. *Rhopalaea hartmeyeri*, recorded only once, generally resembles *R. crassa. Rhopalaea nordgaardi* (> *R. norvegica* Ärnbäck, 1926) is solitary, or up to 2 zooids enclosed in common test. The mechanism of replication is not known. Constriction of the epidermis in the region of the oesophagus (which would involve endodermal tissue from the epicardial sacs) is not impossible (Ärnbäck 1927).

No trace of budding has been found in either *R. crassa* or *R. tenuis* in the course of the present study. Although fairly closely associated individuals are sometimes found, they are never joined, and seldom in contact with one another. Millar (1975) described enlarged terminal ampullae in the abdominal test, and even a differentiated blastozooid 'attached to the abdominal part of the parent' (Millar 1975, p.263). No known mechanism of replication in the Aplousobranchia could account for the presence of such a bud, which could be a juvenile settled on the outside of the test, as in specimens assigned to *Rhopalopsis defecta* Sluiter, 1904 (ZMA TU968.2 < *Rhopalaea crassa*). Salfi (1928) examined many specimens of *R. neapolitana* and could find no buds. He concluded (Salfi 1928, p.370)

> individuals of *R. neapolitana* show phenomena of regression and juvenescence . . . In the regressive phase the zooid is destitute of a branchial sac and connected organs, which will reform by the regenerative process in the phase of rejuvenescence. Following the periods of regression and rejuvenescence an entire modification of the external shape of the individual, and sometimes of the typical shape of the species, occurs.

This conclusion is supported by the present observations on *R. crassa* in which vegetative growth appears confined to regeneration of lost parts of the body, especially of the thorax; and to involve modification of the external shape of the individual as it does in *R. neapolitana*. Thus, in *Rhopalaea*, vegetative replication appears to be at an early stage of development, involving regeneration of parts of zooids, rather than the replication of whole zooids. It is, therefore, very similar to the situation in *Ciona*, which has the capacity to regenerate lost parts of the body from endodermal epicardial tissue (Hirschler 1914). Only in *R. nordgaardi* has the process evolved one stage further toward the aplousobranch pattern — the spontaneous replication of individuals to form a small colony.

Rhopalopsis Herdman, 1890 was erected for species (*R. fusca*, *R. crassa*) closely related to *Rhopalaea neapolitana* Philippi, 1843, but without the minute plications of the branchial sac that had been observed in the type species. This has not been confirmed as a distinction, the minute plications being a variable character, probably dependent on the condition of the specimen. Thus *Rhopalopsis* is now regarded as a junior synonym of *Rhopalaea*.

Rhopalaea piru Monniot and Monniot, 1987 from Tahiti is wrongly assigned. The single specimen for which the species was erected is a small, irregular colony. The zooids have a robust posterior abdominal extension and longitudinal muscles extending onto the abdomen in two strong ventral bands, and from there onto the posterior abdominal extension. *Rhopalaea* is only rarely colonial and then never contains the number of zooids found in *R. piru*. Further, although muscles continue onto the abdomen in *Rhopalaea tenuis*, they do not continue onto a long posterior abdominal extension. These features together with others reported for *R. piru* including the conspicuous oviduct filled with eggs, shallow longitudinal striations in the stomach wall, ventral longitudinal muscle bands terminating against the mid-ventral line, and embedded zooids with their anterior ends only projecting from the surface are all characteristic of *Syndiazona chinensis* Tokioka, 1955a — of which *Rhopalaea piru* is a junior synonym.

Only 2 species of *Rhopalaea* have been recorded from Australia, *R. crassa* with a wide range in the tropical waters of both the eastern and western coasts, and *R. tenuis*, known from many specimens representing a large population in Torres Strait. *Rhopalaea tenuis* is readily distinguished from *R. crassa* by its basal tufts of hair-like roots and the longitudinal muscles continuing onto the abdomen.

Rhopalaea crassa (Herdman, 1880)

(Fig. 4, Plate 1b,c)

Ecteinascidia crassa Herdman, 1880, p. 723; 1882, p. 240.

Rhopalaea crassa: Beneden 1887, p. 21. Tokioka, 1953, p. 210. Millar, 1975, p. 262. Kott and Goodbody, 1982, p. 506.

Rhopalopsis crassa: Van Name, 1918, p. 126.

Ecteinascidia fusca Herdman, 1880, p. 732; 1882, p. 241.

Rhopalopsis fusca: Beneden, 1887, p. 21. Sluiter, 1904, p. 13.

Ciona indica Sluiter, 1904, p. 3 (part, specimen from Station 49 *fide* Hoshino and Nishikawa 1985).

Ecteinascidia (? *Rhopalopsis*) *solida* Herdman, 1906, p. 299.

Rhopalaea sagamiana Oka, 1927b, p. 681.

Rhopalaea macrothorax Tokioka, 1953, p. 212.

? *Rhopalopsis defecta* Sluiter, 1904, p. 14.

Distribution

New Records: Western Australia (Houtman's Abrolhos, QM G11933, WAM 97.78; Cockburn Sd., QM G9670). Queensland (Mooloolabah, QM G10143-5 G11912 G11915; Wistari Reef, QM G10046 GH4105-6; Heron I., QM G9489 G9955-6 G10036 G10089 G10150 G10159 G11899 GH810 GH958 GH2435 GH3463 GH3781; Swain Reefs, QM GH2436 GH2807; Saumarez Reef, QM GH2811; Lizard I., QM GH4078. Philippines (QM GH393 GH408 GH421 GH454 GH477 GH484 GH494 GH515 GH557).

Previously Recorded: Indonesia (Herdman 1880; ZMA TU968.2 TU1258 *Rhopalopsis defecta* Sluiter 1904, Millar 1975). Philippines (Van Name 1918, Millar 1975). Sri Lanka (BM 1907.8.30.3 *E. solida* Herdman, 1906). Japan (Oka 1927b, Tokioka 1953, Millar 1975). Hong Kong (QM G12789 G12808 Kott and Goodbody 1982).

The species is common in coral reef habitats. It is especially common at Heron I. from 2 to 20m depth.

Description

External Appearance: Individuals are elongate, up to 6cm long. The thoracic portion of the body is often 2cm in diameter, but the abdominal portion is usually narrower. The thoracic test may be delicate and almost completely transparent or firm and translucent to opaque. Surface irregularities (that are not present in individuals with thin transparent thoracic test) increase as the thickness and opacity of the test increases. Variations in condition of the test may be associated with age. The test is always opaque and rough over the abdomen. Posteriorly, the abdominal test is expanded and/or extended into solid outgrowths that help to wedge the individual firmly into crevices and spaces in coral rubble. No more than a single zooid is embedded in the test.

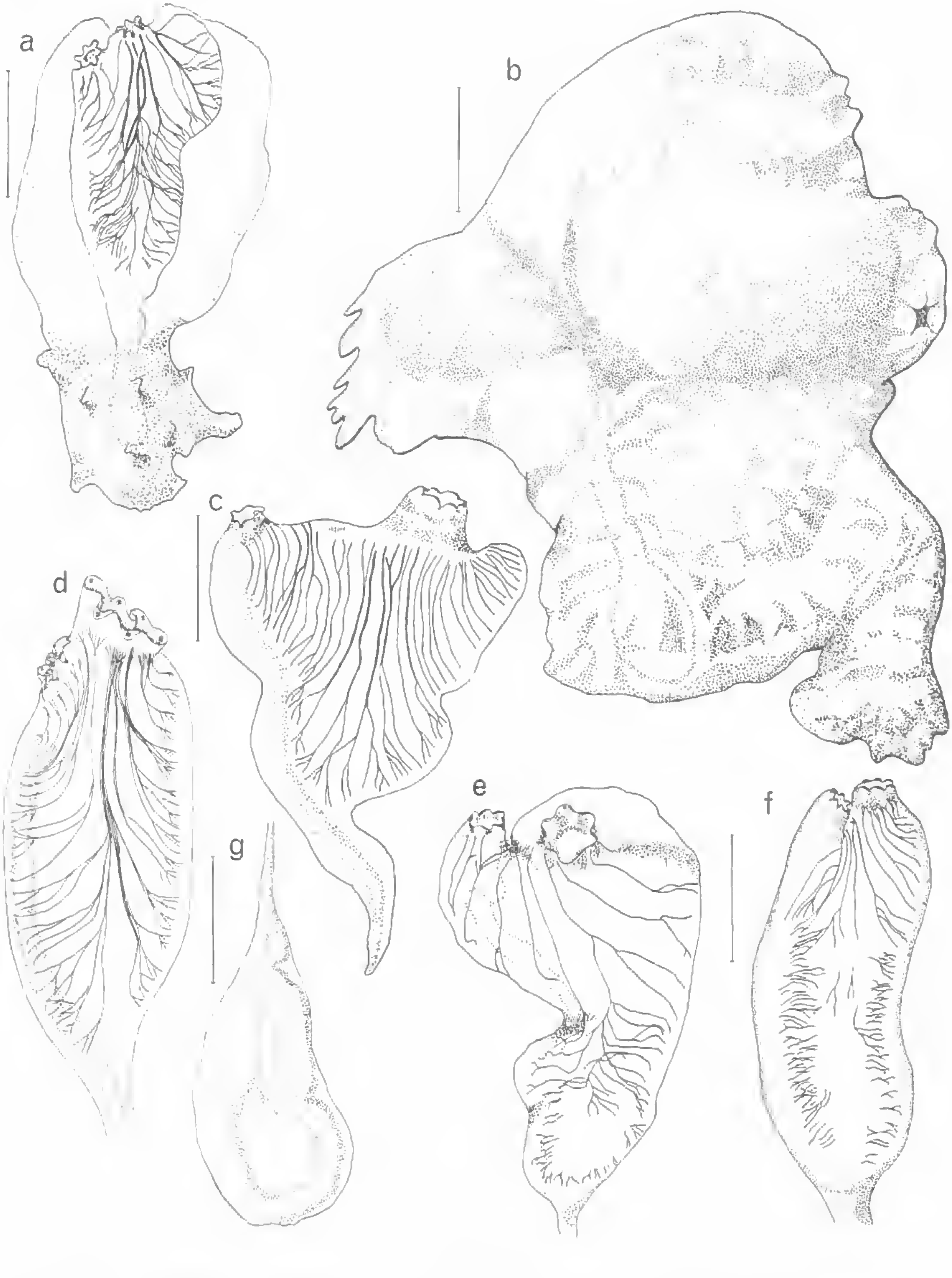


FIG. 4. *Rhopalaea crassa*: **a**, young individual (QM G10159); **b**, aged individual (QM G11912); **c–f**, thoraces showing musculature (QM G 10144 G9921 G10159 G10114 respectively); **g**, gut loop (QM G10144). Scales, a–g, 5mm.

Apertures in specimens with delicate thoracic test are conspicuous when extended. They have 6 prominent lobes and pigment patches between them. Those with solid, gelatinous thoracic test have apertures depressed into the thick test and so concealed by it. The branchial aperture is terminal, and the atrial aperture antero-dorsal, both directed upwards.

Kott and Goodbody (1982) discussed individual colour variations. The conspicuous yellow in the thick thoracic test of apparently older individuals probably indicates the presence of blood cells containing vanadium with an organic ligand that oxidises to olive green when specimens are removed from the substrate (D. Parry *pers. comm.*). Absence of conspicuous colour in both living and fixed specimens with delicate transparent thoracic test is probably a result of the relatively small amount of blood present in the thin test.

INTERNAL STRUCTURE. The thorax is always delicate and the siphons are short, with evenly placed circular muscle bands. The thoracic musculature is primarily longitudinal. Muscle bands from the branchial and atrial siphons break up into a very fine network of fibres at the base of the siphons and join again into 10 to 36 bands extending down the thorax. They divide into branches again across the endostyle, the retropharyngeal groove and across the posterior and dorsal borders of the thorax. One muscle band always originates from the intersiphonal region and divides into ventral and dorsal branches toward the posterior end of the thorax. Terminal branches extend across the endostyle and across the retropharyngeal groove respectively. Muscles are not present on the abdomen.

In one specimen the anterior portion only of the thorax is strongly contracted and the longitudinal muscles appear severed, leaving the terminal branches (where they cross the borders of the body) in position, but leaving only traces of musculature over most of the body wall. In this specimen the internal longitudinal vessels of the posterior end of the branchial sac also are consistently interrupted. The condition of this specimen is consistent with acute contraction of muscles. Its appearance conforms exactly with Tokioka's (1953) description of *Rhopalaea macrothorax*.

There are from 2 to 6 stigmata per mesh, 50 to 100 rows of stigmata, and from 40 to 50 fine internal longitudinal vessels supported on conical papillae. Irregularities occur in the branchial sac. In at least two specimens a part of several rows of stigmata curve to lie longitudinally and some unperforated membrane and irregular interstitial meshes are present in their vicinity. In some specimens from Mudjimba (QM G10144) the internal longitudinal vessels are interrupted between the papillae and the stigmata are small and oval. These thoraces may be regenerating.

The abdomen is tightly enclosed in almost solid test and is only removed with difficulty. The oesophagus is usually fairly long, and expands into a rather rectangular stomach half way down the abdomen. It is smooth externally, but internally the lining is broken up into about 30 distinct fine longitudinal ridges that become irregular only on the dorsal part of the right side of the stomach. The rectum extends anteriorly to open in the anterior third of the peribranchial cavity. The anal border is broken into about 8 rounded lobes. Minute male follicles cluster around the large ovary in the gut loop, posterior to the stomach. Sometimes the abdomen is especially small and may be regenerating. A short vessel extends from the end of the abdomen. It branches in the test, and its terminal ampullae are present in the root-like projections of the test.

REMARKS. The different appearance of specimens with delicate thoracic test and those in which the thoracic test is opaque and irregular, like that covering the abdomen, is pronounced. It is probable that, following loss of the thorax, the test closes and the new thorax regenerates within it. This would explain the extreme irregularity, especially in the orientation of the thorax in these opaque, and presumably older specimens. It is a phenomenon also observed by Salfi (1928 p. 370) for *R. neapolitana* in which there is 'an entire modification of the external shape' (see *Rhopalaea* above).

Paratypes of *Rhopalopsis defecta* Sluiter, 1904 (ZMA TU968.2 Station 310, TU1258 Station 240) are not separable from the present species. The specimens from *Siboga* Station 240 included a group of 3 one attached along the abdominal stalk and another near the base of the third individual, appearing as a colony. The thoraces of a number of these specimens are relatively small, apparently regenerating within firm test continuous with and of the same firm consistency as the abdominal test.

In Australian populations irregular, opaque yellow individuals as well as those with transparent thoraces have been taken from Mooloolabah and Houtman's Abrolhos, as they were from Hong Kong (Kott and Goodbody 1982). However, specimens with delicate transparent tests are most often taken from coral reef locations — only one, opaque-yellow specimen is recorded from Heron

I. (QM GH3463). Perhaps predation occurring in coral reef habitats prevents individuals surviving until the thoracic test becomes thick and opaque. The thorax is missing entirely from a specimen (QM GH2436) from the Swain Reefs.

In addition to yellow, probably associated with intracellular vanadium, both blue and pink individuals have been recorded. One pale blue specimen was taken from the eastern end of Heron I., while populations of this species in the Philippines and Indonesia are a brilliant sapphire blue, as recorded for *Rhopalopsis fusca* Sluiter, 1904. This colour probably results from concentrations of tetrapyrols similar to those causing blue in *Sigillina cyanea* (*pers. comm.* D. Parry). A similar colour is present also in *R. neapolitana* and *R. birkelandi*. Its phylogenetic significance is not understood.

Neither morphology nor colour — both showing considerable variation and overlap — can readily separate most of the known species. Some differences exist in the average number of longitudinal muscles, or number of rows of stigmata, or the size of the abdomen, but they usually do not fall outside the range recorded for *R. crassa*. *Rhopalaea abdominalis* (Sluiter, 1898) from the western Atlantic (see also Van Name 1945, Monniot 1970) is pink to violet-pink in preservative and has fewer rows of branchial stigmata (40) and generally fewer stigmata per mesh (2) than *R. crassa*. *Rhopalaea birkelandi* Tokioka, 1971 from the Pacific coast of South America is deep blue in preservative and has a small abdomen. Specimens of *R. neapolitana* Philippi, 1843, from the Mediterranean (BM 98.5.7.303, AM G4271) and the Adriatic (BM 98.5.7.308) are also blue in preservative and have a relatively large number of longitudinal muscles (about 36). *Rhopalaea hartmeyeri* closely resembles *R. neapolitana*, but is distinguished by its colonial habit.

Rhopalaea tenuis (Sluiter, 1904)

(Fig. 5)

Rhopalopsis tenuis Sluiter, 1904, p.15.

DISTRIBUTION

NEW RECORDS: Queensland (Torres Strait, QM GH4669–74).

PREVIOUSLY RECORDED: Indonesia (Java Sea — Sluiter 1904).

The 5 Siboga specimens were taken at 82m. The new records represent numerous specimens taken by dredge between 9°39′ and 10°03′S and 142°39′ to 142°51′E at 11 to 18m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are soli-

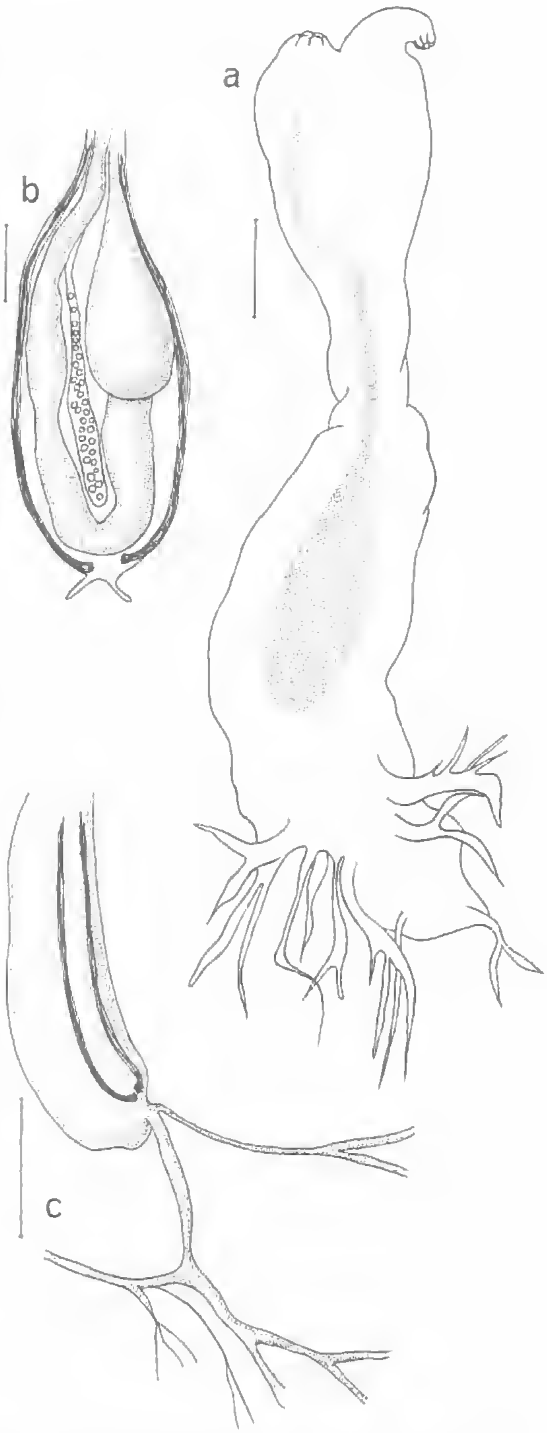


FIG. 5, *Rhopalaea tenuis* (QM GH4669): a, whole individual; b, abdomen showing gut loop, ovary, and muscles from dorsal surface; c, posterior end of abdomen showing muscles from left side. Scales: a,c, 5mm, b, 2mm.

tary, finger-like, upright and up to 6cm long. The thoracic test (upper half to one-third) is delicate, and in newly recorded specimens the thorax is rather mutilated and drawn out, looking rather like a ragged piece of string. The posterior half to two thirds of the test is firm and translucent, with some circular, horizontal wrinkles on the surface. The pinkish abdomen is seen embedded in the upper half of this stalk-like part of the test and blood vessels extend through the lower half. Basally the test is produced into a mass of short, branched root-like structures to which sand adheres, sometimes forming a rounded, sandy hold-fast at the posterior end of the body.

The apertures are on short siphons close together, on the anterior free end of the body. The delicate test of the thorax is produced into 6 rounded lobes around each aperture. The branchial siphon sometimes is turned ventrally, although the thoracic test of the present specimens is usually too mutilated and crushed to determine the actual orientation of the apertures.

In these preserved specimens there is sometimes a trace of reddish pigment in the test, and there are yellow lines along each siphon alternating with the lobes around each aperture.

INTERNAL STRUCTURE: Zooids are delicate with a relatively large and diaphanous thorax and a slightly longer abdomen. The club-shaped abdomen has a narrow oesophageal neck which is about the same length as the swollen, rounded posterior end of the abdomen which contains the stomach and gonads.

The narrow thorax tapers posteriorly. It has about 20 fine longitudinal muscles, about half from the branchial siphon and half from the atrial siphon. These continue as a band along each side of the abdomen abruptly converging posteriorly before terminating in a flat disc, one each side of the mid-dorsal line just anterior to the origin of the test vessel. No transverse muscles were seen.

At the base of the branchial siphon are about 24 fine pointed tentacles, the largest ones alternating with the smaller ones. The flask-shaped neural gland has a short, wide duct with a simple circular opening.

About 12 internal longitudinal vessels on each side of the branchial sac extend the length of the sac and are supported by papillae. There are no secondary papillae. There are about 60 rows of stigmata and about 4 stigmata per mesh.

A simple, vertical gut loop is firmly embedded in the test with the relatively small, oval stomach (sometimes stretched vertically) about half-way down the descending limb. The stomach has a suture line but folds were not detected. The anus opens about two thirds of the way up the branchial sac. A long tubular ovary and numerous male follicles are crowded into the gut loop.

The posterior abdominal test vessel branches in the stalk and the terminal branches extend into the basal root-like projections.

REMARKS. Generally these present zooids conform with the description given by Sluiter (1904).

Sluiter thought individuals possibly were joined together by a basal stolon. However, enough individuals exist in the present collection to establish this does not happen: the species is a solitary one. All *Rhopalaea* have the same narrow waist and their abdomina firmly bedded in solid basal test, however, the branches of the posterior abdominal vessel, and the basal roots of the present species are distinctive. Muscle bands occur on the abdomen in *Rhopalaea nordgaardi* (see Ärnbäck 1927), but not in *R. crassa* or *R. neapolitana*. *Rhopalaea tenuis* is further distinguished by its very much narrower thorax, and fewer thoracic muscle bands and stigmata.

Abdominal muscles, with their circular terminal disc, appear similar to those of the colonial *Syndiazona chinensis* Tokioka 1955a from the Kei Is, the Philippines and the East China Sea (see Millar 1975).

Genus **Pseudodiazona** Millar, 1963

Type species: *Pseudodiazona sabulosa* Millar, 1963a (= *Protopolyclinum claviforme* Kott, 1963).

This rarely encountered diazonid genus is characterised by the presence of a long posterior abdomen containing epicardium, gonads and, at the posterior end, the heart. It has the diazonid characters of internal longitudinal branchial vessels, 6 branchial and 6 atrial lobes, and the anus opening anteriorly at the base of the antero-dorsal atrial aperture. Stomach is smooth, and, possibly as an artifact of its preservation, it sometimes is compressed into a quadrilateral shape in section. Longitudinal muscle bands extend the length of the zooid, from the siphons to the end of the posterior abdomen. Zooids are completely embedded in common test.

A posterior abdomen (present in this genus and in *Tylobranchion*) suggests an affinity with the Polyclinidae. Kott (1963) accordingly included it in *Protopolyclinum* Millar, 1960 (Euherdmaniinae) by expanding Millar's definition of *Protopolyclinum* to include species with complete internal longitudinal branchial vessels as well as those which had only remnants of those vessels in the form of papillae on the transverse vessels (as in the type species *P. pedunculatum* Millar, 1960 from New Zealand). Later in the same year Millar (1963a) described *Pseudodiazona sabulosa*, in the family Diazonidae on the basis of its complete internal longitudinal vessels, and close relationship to the Antarctic *Tylobranchion* — which also has a posterior abdomen.

Millar did not comment on the similarity of his species to *Protopolyclinum claviforme* Kott, with which it is here considered to be conspecific.

Pseudodiazona has affinities with Euherdmaniinae through *Protopolyclinum pedunculatum*. The latter species resembles *Pseudodiazona claviformis* in the shape of its body, and the course of the muscles. Further, although *Protopolyclinum pedunculatum* lacks the internal longitudinal branchial vessels of *Pseudodiazona claviformis*, their rudiments are present as branchial papillae.

Patridium Kott, 1975 originally assigned to Euherdmaniinae, characterised by its internal longitudinal vessels and folded stomach, is a junior synonym of *Pseudodiazona*, the stomach folds being artefacts.

In addition to the type species, one other, *Pseudodiazona abyssa* Monniot and Monniot, 1974 from the eastern Atlantic, has been described.

Pseudodiazona claviformis (Kott, 1963)

(Fig. 6, Plate 1d)

Protopolyclinum claviforme Kott, 1963, p. 72.
Pseudodiazona sabulosa Millar, 1963a, p.718.
Patridium pulvinatum Kott, 1975, p.4.

DISTRIBUTION

NEW RECORDS. South Australia (Seacliff Reef, QM GH2307). Victoria (Off Cape Howe, ZMC 30.9.14). New South Wales (Jervis Bay, QM G10100; Botany Bay, AM Y2149).

PREVIOUSLY RECORDED. South Australia (Northern Great Australian Bight SAM E1035 holotype *Patridium pulvinatum* Kott, 1975). Victoria (Port Phillip Bay BM 85.11.20.34-43 Millar 1963a; Eden Kott 1963).

The species has been taken on rocky substrates at depths of 10 to 100m.

DESCRIPTION

EXTERNAL APPEARANCE. One colony (SAM E1035 holotype *Patridium pulvinatum*) is a large (6cm long) gelatinous, egg-shaped, sessile cushion with some sand on its base. Other colonies are top-, fan- or club-shaped, sometimes with a firm sandy stalk or basal part, and a soft, glassy transparent head wider than the stalk and either rounded or flattened across its upper surface. Sometimes the transparent head of the colony is subdivided into a number of separate lobes of different diameter, and sometimes the whole colony is subdivided, the parts joined at the base of the stalk. Stalked heads are up to 3cm in diameter. Zooids are seen clearly through the glassy test of the top of the colony. Branchial and atrial siphons open separately to the surface by 6-lobed apertures.

INTERNAL STRUCTURE. Zooids are 1 to 4cm long. They are divided into thorax, abdomen and posterior abdomen, the latter being up to two-thirds of the total length. Relatively short vascular appendages (2 or 3) extend out into the test from the posterior end of the posterior abdomen which often is thread-like, but sometimes is drawn up into a broad sac. The branchial aperture is in the centre of the anterior end of the zooid, while the atrial aperture is antero-dorsal. A circular area of the anterior prebranchial body wall surrounding the apertures is white and opaque in preservative and is highly contractile.

The body wall is delicate and quite transparent. Body muscles are longitudinal, about 10 thoracic bands extending posteriorly along each side of the abdomen and posterior abdomen but not onto the vascular appendages. Longitudinal muscle bands branch and bundles of fibres join adjacent bands, to form a wide open and irregular network on each side of the thorax. Commissures between longitudinal muscles alter spacing of the longitudinal bands. In some contracted zooids the bands are evenly spaced, extending more or less parallel to one another. In others, muscle bands curve in an arc from the anterior end, posteriorly along the ventral border of the thorax and then dorsally, where they are crowded together before extending onto the abdomen. In this latter condition, the dorsal border where the muscles are crowded together is strongly contracted and more or less concave while the ventral border is not and extends out in a wide convex arc.

The branchial sac has from 17 to 22 rows of stigmata, with up to 20 per row. About 20 internal longitudinal branchial vessels are supported on short papillae which do not project above the internal longitudinal vessels. The narrow oesophagus opens into a long stomach about halfway down the abdomen. The stomach is smooth externally, but internally its glandular epithelium has longitudinal and irregular interruptions. There is a duodenal area distal to the stomach and a conspicuous oval posterior stomach in the descending limb of the gut. The rectum extends anteriorly to the base of the atrial siphon.

Gonads consist of numerous male follicles and a relatively large ovary. A large number of eggs are sometimes arranged in a single series in the

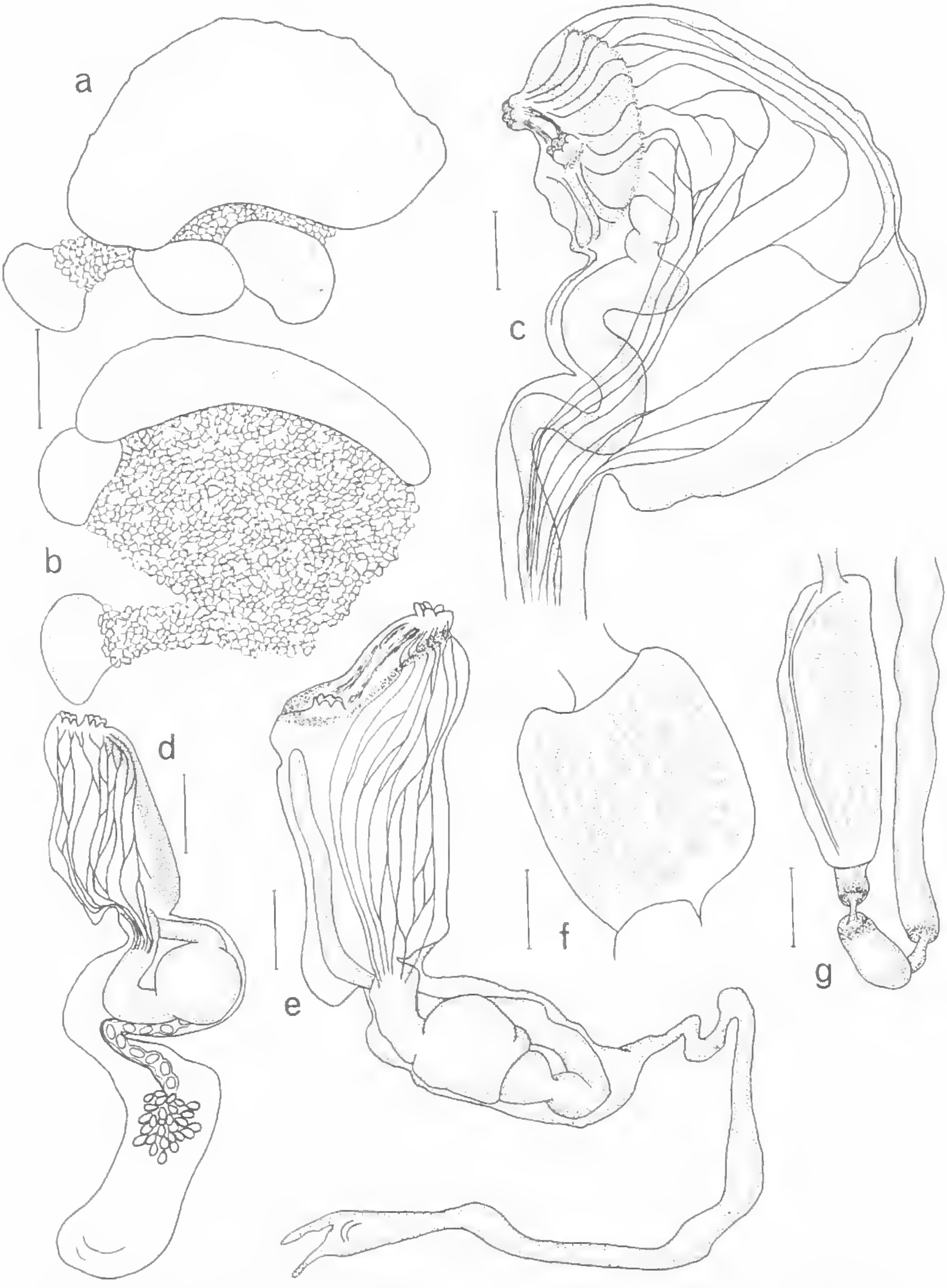


FIG. 6. *Pseudodiazona claviformis*: **a,b**, two views of the one colony (SAM E1035); **c**, thorax (SAM E1035); **d**, whole zooid, with gonads (ZMC); **e**, whole zooid without gonads (SAM E1035); **f,g**, stomach, and posterior end of the gut loop (SAM E1035). Scales: **a,b**, 5mm; **c,e–g**, 0.5mm; **d**, 1mm.

oviduct. In the relaxed posterior abdomen male follicles are arranged serially. However, when contracted, they are bunched anteriorly (ZMC 30.9.14).

REMARKS: Generally, examination of the newly recorded specimens confirms the earlier descriptions. Although Millar (1963a) has not recorded the rather conspicuous branching of thoracic muscles, his specimens have the same numbers and arrangements of muscles, branchial and atrial siphons, rows of stigmata, inner longitudinal branchial vessels, the same stomach lining, anteriorly situated anus, and similar colonies with a glassy transparent and expanded head through which the embedded zooids can be seen.

The species most closely resembles the Antarctic *Tylobranchion speciosum* (see Kott 1969), differing principally in the position of the heart at the end of the posterior abdomen.

Re-examination of the holotype of *Putridium pulvinatum* Kott, 1975, has shown its zooids to be identical with those of the present species. It has the same body proportions, musculature, branchial sac and the same contractile area around the siphons, which, in contracted specimens, flattens the anterior end of the zooid. Kott (1975) completely misinterpreted the stomach structure in these zooids, reporting the stomach as having folds. In fact, the stomach is the same as that in other specimens of *Pseudodiazona*, being basically smooth, but may become folded in some of the preserved zooids. The colony of Kott's (1975) species is large in comparison with recorded specimens of *P. claviformis*. However, in a specimen lot (GH2307) from St Vincent Gulf a reduction in the length of the stalk occurs as colony size increases. The soft top of the colony appears to overgrow the stalk — a trend that probably culminates in large sessile colonies such as the one from the Great Australian Bight (SAM E1035).

Millar (1963a) noted the strong similarity between the present species and *Homoeodistoma longigona* Tokioka, 1959 from Japan. The colonies are the same with a sandy basal portion and a soft upper 'corona' or head. Although Tokioka has not described muscles on other parts of the body, the arrangement of the thoracic muscles in his specimens is similar to that in the present species. The anal opening (opposite the fifth row of stigmata: Millar 1963a), as in all diazonids is well anterior near the base of the atrial siphon, and there are ocelli in the lobes of the atrial siphon (overlooked in the branchial siphon?). Another point of similarity is the large number of eggs serially arranged in the oviduct — a character observed in the two other specimens in which gonads are developed (Kott 1963, and in the newly recorded specimen from Cape Howe — ZMC 30.9.14). However, Tokioka's Japanese species, even if it is found to be a diazonid species, seems more robust than the present species from Australia, and has more thoracic muscles. Further the two species are separated from one another by the tropics.

Family CLAVELINIDAE Forbes and Hanley, 1848

The family contains solitary and colonial species with zooids ranging from the small (less than 1cm long) zooids of *Clavelina minuta* Tokioka, 1962 with only 4 rows of stigmata, up to large (10cm) diazonid-like zooids (e.g. *C. meridionalis*, *C. ostrearium* and others) with very numerous branchial stigmata. Although replication always occurs, some species have solitary zooids while others reflect different degrees of organization, from irregular colonies with separate or partially embedded zooids connected by basal stolons or basal test, to completely embedded zooids regularly arranged in regularly shaped, stalked colonies (*Clavelina baudinensis*, *C. pseudobaudinensis* and the genus *Nephtheis*).

Familial characteristics are smooth bordered apertures opening separately to the exterior; absence of internal longitudinal branchial vessels; wide horizontal membranes between the rows of stigmata; and a well developed posterior abdominal vascular stolon with mesenchymal septum. The vascular stolon branches in the basal test, and the terminal branches end in ampullae from which, usually following their enlargement and isolation from the vascular stolon (Berrill 1935b, 1950), vegetative zooids develop. In some solitary species clones separate from one another and from parental zooids following their formation (e.g. *Clavelina miniata* Watanabe and Tokioka, 1973). In others the adult zooid is resorbed and new zooids develop from the isolated terminal ampullae that persist in the stalk. Thus in the former case clones exist contemporaneously and in the latter case they exist sequentially. Only in the genus *Nephtheis* is the vascular apparatus modified. In this genus it forms a complicated network in the stalk. The site of replication is localised at the top, rather than at the base of the stalk and the terminal ampullae are not isolated from the network at any stage of the replicative process.

As in Diazonidae, the test is translucent and gelatinous, and the body is divided into thorax and abdomen, the latter occupied by the vertical gut loop. Post-mortem colour changes resulting from oxidation of high levels of intracellular vanadium usually result in dark blue zooids.

Body muscles of the Clavelinidae are grouped into longitudinal and oblique bands. The more ventral bands are oblique, extending from the endostyle (rather than from the branchial siphon) toward the postero-dorsal corner of the thorax, where they extend along the abdomen. More dorsal bands are usually longitudinal, extending from the branchial siphon, the intersiphonal region, and, sometimes from the atrial siphon, onto the abdomen. Sometimes muscle bands from the branchial siphon, the intersiphonal region and the endostyle extend to the dorsal border of the body where they appear to fade out as they turn posteriorly, apparently not extending onto the abdomen. These are described below as transverse muscles, although their provenance, from the primarily longitudinal and oblique musculature of the Clavelinidae, is clear. In relaxed thoraces, muscle bands subdivide into separate bundles, exchanging branches with one another. In contracted thoraces these branches draw the separate bundles together causing an apparent decrease in the number of muscle bands resulting in apparent intraspecific variation in the numbers of muscle bands recorded for each species. In the descriptions that follow, the formula developed by Tokioka and Nishikawa (1976) has been used to describe the musculature of clavelinid species. E refers to muscle bands extending from the endostyle, B to muscle bands from the branchial siphon, D to muscle bands from the intersiphonal space between the branchial and atrial apertures, and A refers to muscle bands from the atrial siphon. In species with largely longitudinal muscles, the thorax becomes short and wide with their contraction. Where muscles are primarily oblique, their contraction causes distortion of the thorax, drawing the branchial siphon and endostyle down leaving the atrial siphon at the top of the zooid. Zooids with transverse muscles become long and narrow when contracted.

The length of the abdomen relative to the thorax varies from species to species, although the stomach is usually at its posterior end. The anal aperture is some distance up the branchial sac as in the Diazonidae.

Gonads are present in the posterior end of the gut loop. Eggs are relatively large and numerous (larger than in Diazonidae). The large eggs protrude from the ovarian wall and are rather loosely grouped together amongst the male follicles. The testis consists of numerous pear-shaped follicles, surrounding the ovary and spreading onto the gut wall. In some species fertilisation takes place in the peribranchial cavity where development proceeds. In others, fertilisation is in the distal end of the oviduct, which duly expands and protrudes from the posterior end of the thorax to form a brood pouch in which embryos begin development completing it in the peribranchial cavity before their release as tailed larvae.

Most larvae have a large trunk (0.7 to 1.5mm long), usually with 3 large, triradially arranged adhesive organs, one dorsal and 2 ventral, at the anterior end of the trunk. The adhesive organs are on short, wide stalks and usually consist of a shallow cup of epidermal cells containing a wide but fairly shallow protruding cone of columnar cells. These increase in length toward the centre to form the cone. Occasionally the epidermal cup is absent (*Clavelina baudinensis*), and in several species the adhesive organs are much modified (see *C. dagysa*). The adhesive organs are supported on a stalked frontal plate. The stalk of the frontal plate is horizontal, extending from the posterior abdominal end of the oozooid. The plate is more or less flattened and stands vertically against the anterior end of the oozooid. Frontal plate and stalk, together with the developing oozooid, are all in the larval trunk and enclosed by test. An otolith and an ocellus are in the cerebral vesicle. Usually the tail encircles the trunk around the mid-line. Anteriorly it passes up between the 2 lower adhesive organs and to the right of the upper one. Two, 4, or more, rows of stigmata develop in larvae before their liberation. However the gut loop is only partially differentiated and completes its development after larval release.

Despite the general similarity of clavelinids and diazonids, a cionid-like ancestor is most likely for Clavelinidae, for in *Ciona* a similar mesodermal septum develops in the posterior abdominal vascular stolon (Millar 1953a) and in some cases the stolon itself is well developed (e.g. in *Ciona intestinalis longissima* and *C. intestinalis gelatinosa*: see Van Name 1945). In Diazonidae the posterior vascular stolon never has a mesodermal septum, and an origin from some pre-cionid ancestor, through exploitation of the regenerative capacity of the epicardium for replication is possible; while Clavelinidae exploited the mesodermal septum of Cionidae for the same purpose.

Pycnoclavella Garstang, 1891 and a new monotypic genus *Euclavella* (type species *Colella claviformis* Herdman, 1899) are separated from Clavelinidae by their invaginated, tubular, larval adhesive organs. This suggests a different origin, but probably also from a cionid ancestor. These genera are further distinguished from Clavelinidae by their smaller zooids, fertilisation at the base of the oviduct, smaller gonads, and probably a different method of replication — *viz.* horizontal division of the abdomen (see below). *Stomozoa* Kott, 1957b, also previously thought clavelinid, has many characters separating it from this family (see below, Stomozoidae). *Archiascidia* Julin, 1904, from the Mediterranean, previously thought a monotypic clavelinid, is probably a synonym of *Pycnoclavella.*

Only 2 genera of the Clavelinidae are recognised in the present work, *viz. Clavelina* and *Nephtheis*, separated from one another by the vascular network in the latter. Records of *Nephtheis* (monotypic) are at present confined to the tropical western Pacific. *Clavelina*, a relatively diverse genus with a cosmopolitan range is well represented in Australian waters. Records of the family from the Antarctic are confined to a single zooid, probably in the genus *Clavelina* (see Kott 1969, *Podoclavella* sp.); and affinities of Australian representatives of the genus are probably with the tropical fauna.

Genus **Clavelina** Savigny, 1816.

Type species: *Ascidia lepadiformis* Mueller, 1776.

The genus is here defined as comprising solitary or colonial species of the Clavelinidae in which the zooids are connected by basal stolons, or completely or partially embedded in common test. The thorax is large with not less than 4 rows of stigmata and not less than 20 stigmata per row. Posterior abdominal vascular stolons branch but do not form a network. Replication is from isolated terminal ampullae of the vascular stolon in the basal test. Eggs are fertilised and begin development in the distal part of the oviduct which is enlarged to form a brood pouch at the posterodorsal corner of the thorax or in the anterior part of the abdomen; and they continue their development in the peribranchial cavity.

Savigny (1816) defined this genus as having a stalked body, branchial and atrial openings without lobes, with neither folds nor papillae in the branchial sac, with languets on the dorsal lamina, and with an abdomen containing the gut loop and ovary posterior to the thorax. Milne Edwards (1842) added its capacity to replicate to the generic definition. This generic definition is, in fact, a recitation of family characteristics. *Clavelina*, as defined, includes a wide range of forms from the solitary zooids of *C. meridionalis* to massive colonies.

The type species, *Ascidia lepadiformis* (Mueller, 1776), has, in addition to other clavelinid characters, separate zooids arising from common basal test. *Podoclavella* Herdman, 1890 was subsequently erected to accommodate solitary species such as *Clavelina meridionalis*; and *Stereoclavella* Herdman, 1890 accommodated species such as *C. australis* with separate zooids but with the basal test forming a solid mass or common stalk. *Synclavella* Caullery, 1900, was erected to accommodate clavelinid species in which the zooids were completely embedded.

Subsequently Van Name (1945) and Berrill (1950) drew attention to the difficulty in separating genera on the basis of the degree to which their zooids were separated, a view with which the present author is in agreement.

Huus (1937) separated *Podoclavella* and *Clavelina* on the basis of the presence of structural ridges on the stomach in the latter genus. However, again, the attempt to subdivide the genus was unsatisfactory and probably invalid — *Clavelina lepadiformis* has a stomach that is rectangular in section but there do not appear to be any structural ridges. Nishikawa and Tokioka (1976, p. 63) in a review of some clavelinids in Japanese waters observed, that 'the feature of the stomach seems to differ considerably according to the physiological state of the zooids'. In the present study, the presence of structural ridges in the stomach is variable in *Clavelina meridionalis, C. moluccensis*, and *C. robusta* n.sp.

Accordingly there does not appear to be any justification for the subdivision of *Clavelina* as originally defined either on the basis of its stomach or the degree to which its zooids are free or embedded. Accordingly *Podoclavella, Stereoclavella* and *Synclavella* as well as *Chondrostachys* MacDonald, 1858 are regarded as junior synonyms of the genus.

Of the 14 species of *Clavelina* recorded from Australia, *C. australis, C. baudinensis, C. cylindrica, C. dagysa, C. mirabilis, C. ostrearium, C. pseudobaudinensis* and *C. nigra* n.sp. are indigenous Australian species and are all temperate. *Clavelina arafurensis, C. fecunda, C. moluccensis, C. meridionalis, C. robusta* n.sp and *C. oliva* n.sp. are tropical western Pacific species, although *C. moluccensis* has a range into temperate Australian waters.

The genus is not known from the Antarctic and the affinities of Australian species are with tropical taxa. Australian indigenous species are temperate, but they have recognizable phylogenetic affinities with tropical, possibly sister, species — *viz. Clavelina australis* with *C. robusta*; *C. cylindrica* and *C. nigra* n.sp. with *C. moluccensis*; *C. dagysa* and *C. ostrearium* with *C. oliva* n.sp. Generally, the species appear to be prolific, the large zooids incubating large numbers of embryos. When liberated, the larval trunk is large and both adult organs and adhesive apparatus are well developed but the tail does not suggest a strong swimming capability. Lack of dispersal may explain the high level of speciation evident in Australian temperate waters.

KEY TO THE SPECIES OF *CLAVELINA* RECORDED FROM AUSTRALIA

1. Colonial, the colony regular and rope-like; a short narrow cylindrical neck separates each zooid from the common test mass . . . . *C. cylindrica*
   Colonial or solitary, colonies not regular and rope-like; no short, narrow, cylindrical neck separates zooids from the common test mass 2
2. Zooids partially or completely embedded in common test 3
   Zooids solitary or united only by thin vascular stolons 4
3. Zooids not almost completely embedded (at least whole of thorax projecting) 7
   Zooids almost completely embedded (not more than anterior part of thorax projecting) 12
4. Zooids long, extending to base of stalk; vascular appendages short 5
   Zooids long or short, never extending to base of stalk; vascular appendages long 6
5. Stalk thin and leathery . . . . . . *C. ostrearium*
   Stalk not thin and leathery . . . . . . *C. dagysa*
6. Transverse muscles present anteriorly; oblique muscles posteriorly . . . . *C. meridionalis*
   Transverse muscles not present anteriorly; muscles longitudinal and oblique . . . . *C. oliva* n.sp.
7. Thoracic muscles all transverse; muscles inconspicuous on the abdomen 8
   Thoracic muscles not all transverse; muscles conspicuous on the abdomen 9
8. Pigment patches in a transverse row of 3 between the apertures . . . . *C. moluccensis*
   Pigment patches not in a transverse row of 3 between the apertures . . . . *C. nigra* n.sp.
9. Oblique muscle bands < twice the number of branchial muscles (E<2B) . . . *C. fecunda*
   Oblique muscle bands > twice the number of branchial muscles (E > 2B) 10
10. Thoraces only free of common test . . . . *C. mirabilis*
    Thoraces and at least part of abdomen free of common test 11
11. Thoracic muscles about 10; median pigment patches alternate with apertures . . . . *C. australis*
    Thoracic muscles about 20; no median pigment patches alternating with apertures . . . . *C. robusta* n.sp.
12. Muscle bands all longitudinal . . . . *C. baudinensis*
    Muscle bands not all longitudinal 13
13. Colony a regular mushroom-shape . . . . *C. pseudobaudinensis*
    Colony not a regular mushroom-shape . . . . *C. arafurensis*

In addition to the species already recorded from Australia, the following have been recorded from the western Pacific region and may occur in Australian waters.

Clavelina coerulaea Oka, 1934 from Japan has a colony that resembles that of *C. viola*, its zooids being separate and narrowing to their points of attachment to the basal stolons (see Nishikawa and Tokioka 1976). Although, its musculature generally resembles that of *C. moluccensis*, having neither oblique nor longitudinal muscles, it has a few anomalous muscles that cross the thorax from the atrial siphon in the opposite direction to the majority of the muscle bands. Living, the species is translucent blue with darker blue bands around the apertures.

Clavelina cyclus Tokioka and Nishikawa, 1975 from Okinawa and the Philippines (QM GH475) consists of zooids partially embedded in common test, with a muscle formula 4E, 8B, 2D (Nishikawa and Tokioka 1976). In life these zooids are grey with a white band around the base of the branchial siphon. Their colour resembles that of the zooids of *C. nigra* n.sp. The species are clearly distinguished by their muscles which, in *C. nigra*, are all transverse.

Clavelina elegans (Oka, 1927a) from Japan (see Tokioka and Nishikawa 1976, and Nishikawa and Tokioka 1976) has zooids of 2 to 3cm joined by common basal test, with muscle formula 4-6E, 4B, 2-4D. All muscle bands extend along the abdomen. The species resembles *C. fecunda* in its colony and zooid musculature. *C. elegans* is distinguished by its larger zooids and larvae and by the absence of yellow in the living zooids.

Clavelina enormis Herdman, 1880, from the western Indian Ocean and South Africa, has long (5cm) zooids attached to branching stolons or to a common basal stalk. It resembles *C. australis*, but is distinguished from it by a

TABLE 1. SUMMARY OF CHARACTERS OF THE SPECIES OF *CLAVELINA* RECORDED FROM AUSTRALIA

Species	[1]Biogeographic description	[2]Range around Australia	[3]Colony organis-ation	Colour (living)	Muscles	Prestomach	Larval trunk (length, mm)	Other
C. dagysa	A,te	Rottnest I.–Geographe Bay	S	solid blue	>20E 3B 3D	none	1.3	short vascular stolon
C. ostrearium	A,te	Albany–Nuyts Arch.	"	"	20E 10B 5D	"	1.25	"
C. meridionalis	WP,tr	Port Hacking–Dampier Arch.	"	lateral yellow patches	>20E 2B 2D	"	1.1	long vascular stolon
C. oliva n.sp.	WP,tr	Lindeman I.–Dampier Arch.	"	"	10E 5B 2D 4A	"	1.0	"
C. fecunda	WP,tr	Heron I.–Rottnest I.	ES	"	7E 5B 3D	"	0.75	embryos numerous, zooids small
C. robusta n.sp.	WP,tr	Lizard I.–Abrolhos	"	"	8E 3B 3D	"	1.3	—
C. mirabilis	A,te	South Australia	"	?	7E 8B 1D	"	?	transverse muscle crosses thorax
C. australis	A,te	Westernport Moreton Bay	"	median blue patches alternate with apertures	7E 2B 2D	"	0.7	with white dots in living test
C. cylindrica	A,te	Shark Bay–Westernport	"	"	10E 10B 4D	present	1.2	rope-like colony, short abdomen
C. moluccensis	IWP,tr-te	Exmouth Gulf–Lizard I.	"	3 blue patches in transverse line between apertures	>20E 3B 3D	"	1.2	short abdomen
C. nigra n.sp.	A,te	Rottnest I.	"	"	>20E 4B 2D	"	?	"
C. baudinensis	A,te	Rottnest I.–Albany	E	"	0E 9B 0D 2A	none	0.5	–
C. pseudobaudinensis	A,te	Abrolhos–Lord Howe I.	"	transverse blue line or median patches between apertures	6E 3B 0D 3A	"	0.9	with white dots in living test
C. arafurensis	WP,tr	N. Australia	"	lateral yellow patches	6E 4B 2D	"	?	–

[1]A, indigenous; WP, Western Pacific; IWP, Indo-West Pacific; tr. tropical; te, temperate. [2]Range given anticlockwise around the continent. [3]E, zooids entirely embedded; ES, zooids partially embedded; S, zooids solitary.

relatively small number of endostylar muscles (4) and a leathery basal stalk.

Clavelina miniata Watanabe and Tokioka, 1973 from Japan has solitary zooids that separate from the parent zooid immediately following replication. The longitudinal and oblique muscles are equally numerous, distinguishing the zooids from those of *Clavelina oliva* n.sp. which has more oblique than longitudinal bands.

Clavelina minuta Tokioka, 1962 from Japan has only 4 rows of stigmata and is clearly distinct from all other species.

Clavelina obesa Nishikawa and Tokioka, 1976 from Japan and the Philippines (QM GH523, GH554, GH560) has rather stout zooids up to 2cm that, like *C. viola*, are attached to basal stolons. However *C. obesa* does not have the tapering stalk of *C. viola*, it is much smaller and its muscles are principally transverse, confined to the thorax. In the latter character it resembles *C. moluccensis* but it has fewer muscles, and in life it is bluish-white without the characteristic pigment patches of *C. moluccensis*.

Clavelina viola Nishikawa and Tokioka, 1976 from southern Japan and the western Pacific (Nishikawa 1984) forms colonies of zooids (up to 4cm long) that narrow to basal stolons. The zooids closely resemble those of *Clavelina oliva* n.sp. which, however, is distinguished by its solitary or near-solitary habit.

Podoclavella polycitorella Tokioka, 1954a from the Tokara Is and the western Pacific (Nishikawa 1984) has a polyclinid larva (Nishikawa *loc. cit.*), and may be a species of Euherdmaniinae with 8 rows of stigmata.

Clavelina flava Monniot, 1988 from New Caledonia has thread-like zooids with a long oesophagus, the anus opening at the base of the atrial cavity, small ovary, large testis follicles and embryos developing in the oviduct — all characters indicative of *Pycnoclavella* or *Euherdmania* rather than *Clavelina*. Further, the larvae lack the axial cone of the adhesive organs of *Clavelina*. They may have partly everted tubular adhesive organs. The ocellus is large, and although an otolith is reported, it is not shown on the figure (Monniot 1988, fig. 3H). Colonies resemble those of *Pycnoclavella arenosa* n.sp., with sand adhering around the common stalk. However, zooids have more stigmata — 10 to 12 rows instead of the maximum of 6 (in *P. arenosa*), the stomach is folded rather than smooth as in *Pycnoclavella*, and the siphons have lobed rather than smooth rims. Thus, although the species has gonads in the abdomen, it appears to have closer affinities with *Euherdmania* than *Clavelina* or *Pycnoclavella*.

Clavelina arafurensis Tokioka, 1952
(Fig. 7. Plate 1e,f)

Clavelina (*Synclavella*) *arafurensis* Tokioka, 1952, p.97. Nishikawa, 1984, p. 116.

DISTRIBUTION

NEW RECORDS: Western Australia (Exmouth Gulf, QM G11987 8), Philippines (QM GH449 GH478).

PREVIOUSLY RECORDED: Arafura Sea (Tokioka 1952), Truk (Nishikawa 1984).

The colonies are found under ledges.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of lobes containing up to 12completely embedded zooids extending parallel to one another to open on the upper surface where they project slightly. Lobes up to 1cm high and about 0.5cm in diameter branch off an irregular, branching, basal stalk.

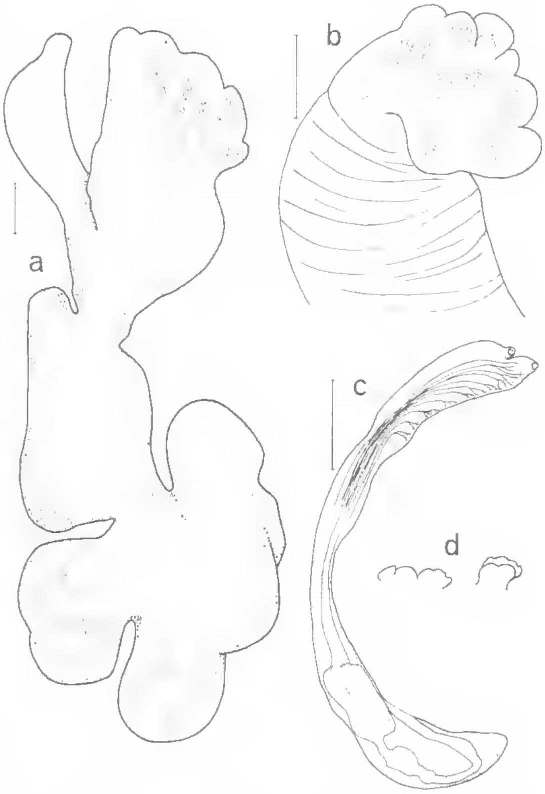


FIG. 7, *Clavelina arafurensis*: **a,b**, colonies (QM G11988 G11987); **c**, zooid (QM G11987); **d**, anal border, opened out and entire (QM G11987). Scales: **a,b**, 2mm; **c**, 1mm.

The glassy, upper thoracic portion of each lobe is slightly wider than the firm, translucent basal part. Vascular stolons of the zooids extend through the basal stalk, where new vegetatively produced zooids grow up into new, vertical zooid-bearing lobes.

In life zooids are purple with regular bright yellow triangular patches on each side of the dorsal midline between the siphons. The apex of each patch is at the side of the atrial siphon, and the rounded base of the triangle spreads around the base of the branchial siphon. There may also be a yellow streak along the dorsal surface.

Internal Structure: Zooids are relatively small, about 0.6cm long, of which thorax, oesophageal neck and posterior expanded part of the abdomen are all about one third. Apertures are on short siphons, the branchial aperture turned slightly ventrally and the atrial aperture directed upwards. About 12 muscle bands on the thorax have formula 6E,4B,2D. These extend along the abdomen. There are about 32 tentacles in 3 concentric circles with the 8 large tentacles near the base of the branchial siphon, 8 moderate sized tentacles in the middle circle, and 16 small ones in the anterior circle. The neural gland opening is long and vertical, protruding slightly into the pharynx.

There are 12 to 16 rows of 20 to 30 stigmata. The oesophagus is long, prestomach absent, and the large, roomy stomach is in the anterior half of the posterior third of the zooid. It has 4 or more, sometimes irregular, rounded folds, apparently artefacts. A small, oval posterior stomach occurs before the gut curves around to open into the rectum at the posterior end of the zooid. The anal opening is bilabiate, the mesial lip with irregular, shallow lobes and the lateral lip with 2 smooth lobes. Gonads are present in the gut loop, although the newly recorded specimens are not mature. Larvae are unknown.

Remarks: Colonies and zooids, including pigmentation of the newly recorded specimens, are identical with those previously recorded from the Arafura Sea. The species has smaller zooids than is usual for many species of *Clavelina*, and colonies are less regular than is usual for species with completely embedded zooids. The stomach resembles that of *Clavelina oliva* n.sp. but is further toward the posterior end of the abdomen. The arrangement of the thoracic muscles also resembles that in *C. oliva*, however they are not so numerous. Zooids and their muscle bands also resemble those of *C. elegans*. However, the small completely embedded zooids and irregular colony together distinguish this species from all others.

Clavelina australis (Herdman, 1899)

(Fig. 8, Plate 2a–c)

Stereoclavella australis Herdman, 1899, p. 6.
Podoclavella australis: Kott, 1957a, p. 93 (part, specimen from Port Jackson); 1972c, p. 234; 1972d, p. 242.
Not *Synclavella australis*: Caullery, 1900, p.1419 (? < *Clavelina pseudobaudinensis*).

Distribution

New Records: ? Victoria (Western Port, MV F53399). New South Wales (Ulladulla, QM G11953; Port Hacking, AM Y2142 Y2145 Y2154–5). Queensland (Moreton Bay, QM G9250 G9253–4 G9256 GH3890).

Previously Recorded: New South Wales (Port Hacking — AM Y814 Kott 1972c; Port Jackson — holotype AM U132, AM G63, Herdman 1899, Kott 1957a).

Description

External Appearance: Colonies vary from top-shaped with a thick stalk, the upper 1cm of the zooids fanning out from the upper surface of the stalk in which the posterior ends of zooids are embedded; to massive colonies in which the whole length of the long cylindrical zooids (up to 4cm) are separate from one another arising from a basal plate of common test about 4mm thick. Both sorts of colony have been taken from Moreton Bay. However, the latter type in which the zooids are separate from one another has been taken only from Moreton Bay.

Living colonies are always conspicuous, with yellow to yellowish-blue zooids in transparent test with three large bright blue patches in the median line — one over the anterior end of the endostyle, one between the siphons and one posterior to the base of the atrial siphon. There is a smaller patch of bright blue over the anus and white spots on anterior parts of the test.

Internal Structure: Zooids are robust, with a relatively long, narrow oesophageal neck joining the thorax to the expanded (and often embedded) posterior end of the abdomen (containing the stomach, gut loop, gonads and heart). Body muscles are strong, although not particularly numerous, with the formula 7E,2B,2D. They continue to the posterior end of the abdomen, those on the left extending around to the ventral border and those on the right extending dorsally behind the stomach. There are 12 short, stumpy branchial tentacles. The vertical slit opening of the neural duct protrudes slightly into the pharynx. There are 14 to 18 rows of 50 to 75 stigmata. There is no prestomach, and the stomach is about three quarters of the way down the abdomen. It has a suture line and sometimes wraps around each side of the intestine. The anus opens into the posterior-third of the atrial cavity. Gonads are

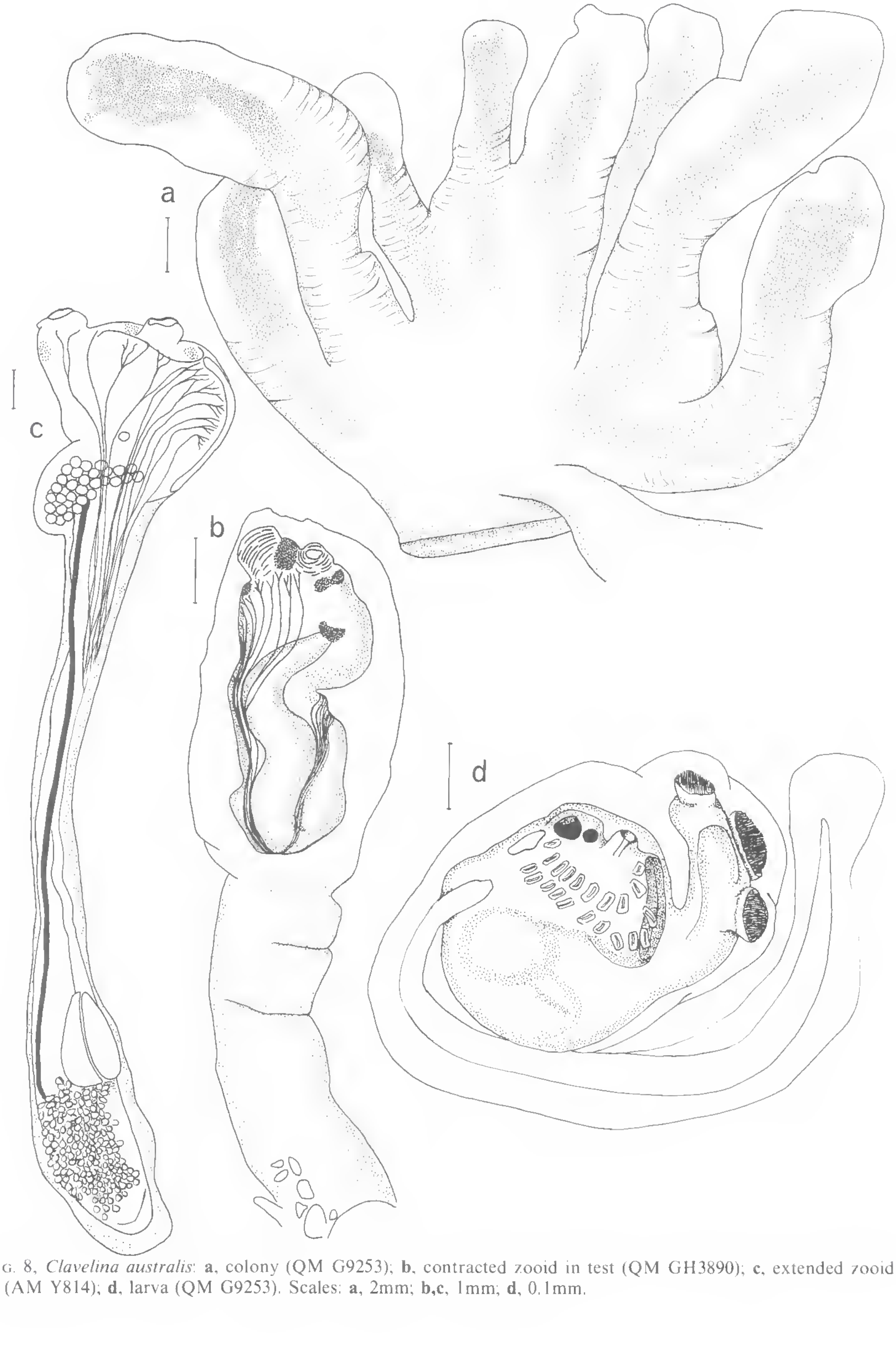


FIG. 8, *Clavelina australis*: **a**, colony (QM G9253); **b**, contracted zooid in test (QM GH3890); **c**, extended zooid (AM Y814); **d**, larva (QM G9253). Scales: **a**, 2mm; **b,c**, 1mm; **d**, 0.1mm.

in the gut loop, male follicles, as usual, covering and obscuring the ovary.

When breeding, up to 100 embryos are present in a brood pouch that extends across the posterior end of the right side of the thorax from the posterodorsal corner. Embryos complete their development in the peribranchial cavity. Colonies from Port Hacking (AM Y84) in June have embryos in the brood pouch and atrial cavity in June. Moreton Bay populations collected in May and July also have embryos, although those from Ulladulla in July do not.

Larvae are smaller than is usual for this genus. The trunk is about 0.7mm long, with the tail wound about three quarters around it. Sometimes the tail crosses the anterior end of the larva from left to right forcing the 2 adhesive organs on its left upwards and the one on its right downwards. The frontal plate is well developed, with slight lobes alternating with adhesive organs. Adhesive organs have a shallow epidermal cup surrounding a wide, shallow axial cone.

REMARKS: The species is large, with long zooids, resembling those of the new tropical species *C. robusta* n.sp. The species are distinguished by their musculature, pigmentation and larvae. Larvae of the present species are much smaller than those of the new species. The large zooids of the present species also resemble those of some larger specimens of *C. moluccensis*. The longitudinal and oblique muscles distinguish it, *C. moluccensis* having conspicuous transverse muscle bands only. *Clavelina moluccensis* can also be distinguished from *C. australis* by its transverse row of 3 pigment patches between the siphons and by its prestomach. Living specimens of *C. pseudobaudinensis* have the same white spots in the test as the present species, although zooids of *C. pseudobaudinensis* are completely embedded.

Clavelina enormis Herdman, 1880 from southern and eastern Africa (see Michaelsen 1930, Millar 1975) has long (5cm) zooids rising from a common basal mass of test that is sometimes modified into a common stalk. The species resembles *C. australis* in the size and form of its colony, zooids, larvae and their brood pouch. However, *C. enormis* apparently has only about 4 endostylar muscles, and basally the stalk becomes very leathery, while in *C. australis* the stalk or basal test is gelatinous and there are twice the number of endostylar muscles. Further, the known range of *C. australis* suggests that the species are not conspecific, *C. enormis* being recorded only from the eastern Indian Ocean while *C. australis* is known only from subtropical to temperate latitudes off the eastern Australian coast. Michaelsen (1930) recorded *C. enormis* from Oyster Harbour, Albany (Western Australia), but again the record seems anomalous; the specimen is probably one of *C. moluccensis* (known from Albany).

A single, possibly juvenile zooid, with the median pigment patches and musculature characteristic of this species, has been taken from Western Port (Victoria) and could be of this species, suggesting its range may extend further south than Ulladulla.

Clavelina baudinensis Kott, 1957

(Fig. 9, Plate 2d)

Clavelina baudinensis Kott, 1957a, p. 87 (part, specimens from Rottnest I. with small larvae); 1972b, p. 166 (part, specimens from Rottnest I.). **Not** Millar, 1966a, p. 363; Kott 1972a, p. 4 (< *C. pseudobaudinensis*).

DISTRIBUTION

NEW RECORDS: Western Australia (Rottnest I., WAM 30.75; King George Sound, WAM 22.87).

PREVIOUSLY RECORDED: Western Australia (Rottnest I. — holotype AM Y801, paratypes AM Y1118 Kott 1957a, 1972b).

The species has been taken from 2 to 12m.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of mushroom-shaped heads of soft, glassy test, onto which the zooids open, supported on firm, sometimes gelatinous, but often hard and leathery, stalks up to 5cm long and 1 to 1.5cm in diameter. The lower part of each stalks divides into short holdfasts or long prop-like branches (WAM 22.87). Sometimes the top of the stalk is divided so the head of the colony separates into lobes. Zooids are completely embedded, the test being only slightly raised over the upper part of thorax on the upper surface of the mushroom-shaped head of the colony. Zooids are up to 3cm long, and quite robust. They extend down into the firm test at the top of the stalk.

Living colonies are white and translucent with one blue patch over the endostyle, 3 in a transverse arc ventral to the base of the atrial siphon, and a pair (one on each side) behind the base of the atrial siphon.

INTERNAL STRUCTURE: The zooid is long and narrow, with a large roomy thorax slightly longer than the posterior expanded part of the abdomen containing stomach and gonads. The oesophageal neck is long and narrow, occupying about two-thirds of the total length of the abdomen. Body musculature is unusual as both dorsal and endostylar muscles are absent, although there are 2 bands with branches extending along the dorsal side of the atrial siphon and a branch from one of these crosses the intersiphonal area together with a branch from one of the branchial siphon muscles. Thus, the muscles are all longitudinal, with formula OE,9B,OD,2A. Muscles extend from the thorax along the length of the abdomen. There are 6 large, 6 middle-sized and 12 small rudimentary tentacles respectively in 3 concentric rings at the base of the branchial siphon. The opening of the neural gland is a vertical slit between two protuberant fleshy lips.

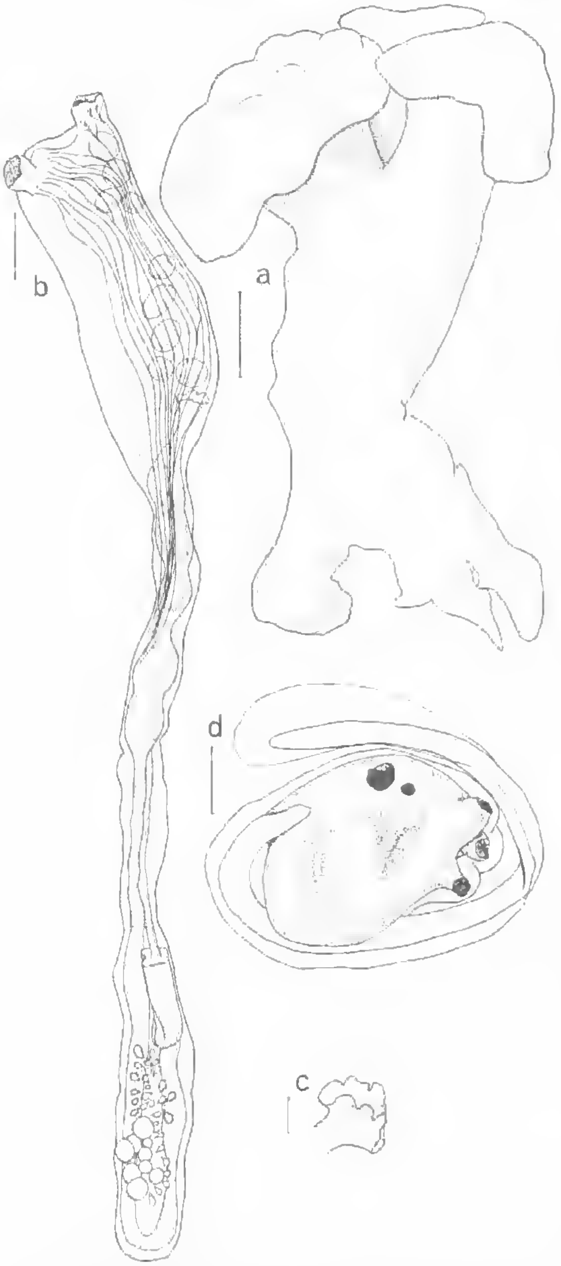


FIG. 9. *Clavelina baudinensis*: a. colony (WAM 30.75); b. zooid (holotype AM Y801); c. anal border (holotype AM Y801); d. larva (holotype AM Y801). Scales: a. 5mm. b. 1mm; c,d. 0.1mm).

There are 17 to 20 rows of 50 to 60 stigmata. The oesophagus is long, and prestomach absent. The stomach, in the anterior half of the posterior expansion of the abdomen, is long and narrow. It has a suture line, but no other structural ridges although in section it is more or less rectangular with one concave side where it lies against and curves slightly around each side of the intestine. An oval, posterior stomach enlargement in the descending limb of the gut. The ascending limb is occupied entirely by the rectum. The anal opening, near the posterior end of the atrial cavity, is bilabiate and each lip is irregularly lobed.

The ovary contains large eggs, 0.3mm in diameter. These develop in the atrial cavity, where they are crowded in some zooids of the holotype (collected in November).

Larvae are small, the trunk only 0.5mm and the tail completely encircles it. Adhesive papillae lie triradially, each a group of modified ectodermal cells on the end of a short stalk projecting from a short frontal plate at the anterior end of the larval trunk.

REMARKS: Kott (1976), in describing *C. pseudobaudinensis*, refers to colonies of the present species containing the characteristic small larvae, from Laverton Bay. This is an error — there are no colonies of *C. baudinensis* from that location. Records of the species are confined to the south-western corner of western Australia from Rottnest I. to King George Sound, and apparently the species is indigenous to that area. The species can be distinguished from *C. pseudobaudinensis* — which has a similar colony — by its unique thoracic muscle formula, distinctive arrangement of blue pigment patches, and its small larvae. There is no other species that completely lacks endostylar muscles, although *C. fecunda* has very few. Nevertheless, this does not indicate a relationship between these two species, for they are separated by many other characters.

Clavelina cylindrica (Quoy and Gaimard, 1834)
(Fig. 10, Plate 2e,f)

Polyclinum cylindricum Quoy and Gaimard, 1834, p. 618.

Chondrostachys sp. MacDonald, 1858, p. 401.

Chondrostachys macdonaldi Bronn, 1862, Taf. 16 figs 1–7. Hartmeyer 1909, p. 1427.

Chondrostachys (*cylindrica*): Caullery, 1908, p. 229; 1909, p.52.

Chondrostachys cylindrica: Hartmeyer 1909, p. 1427.

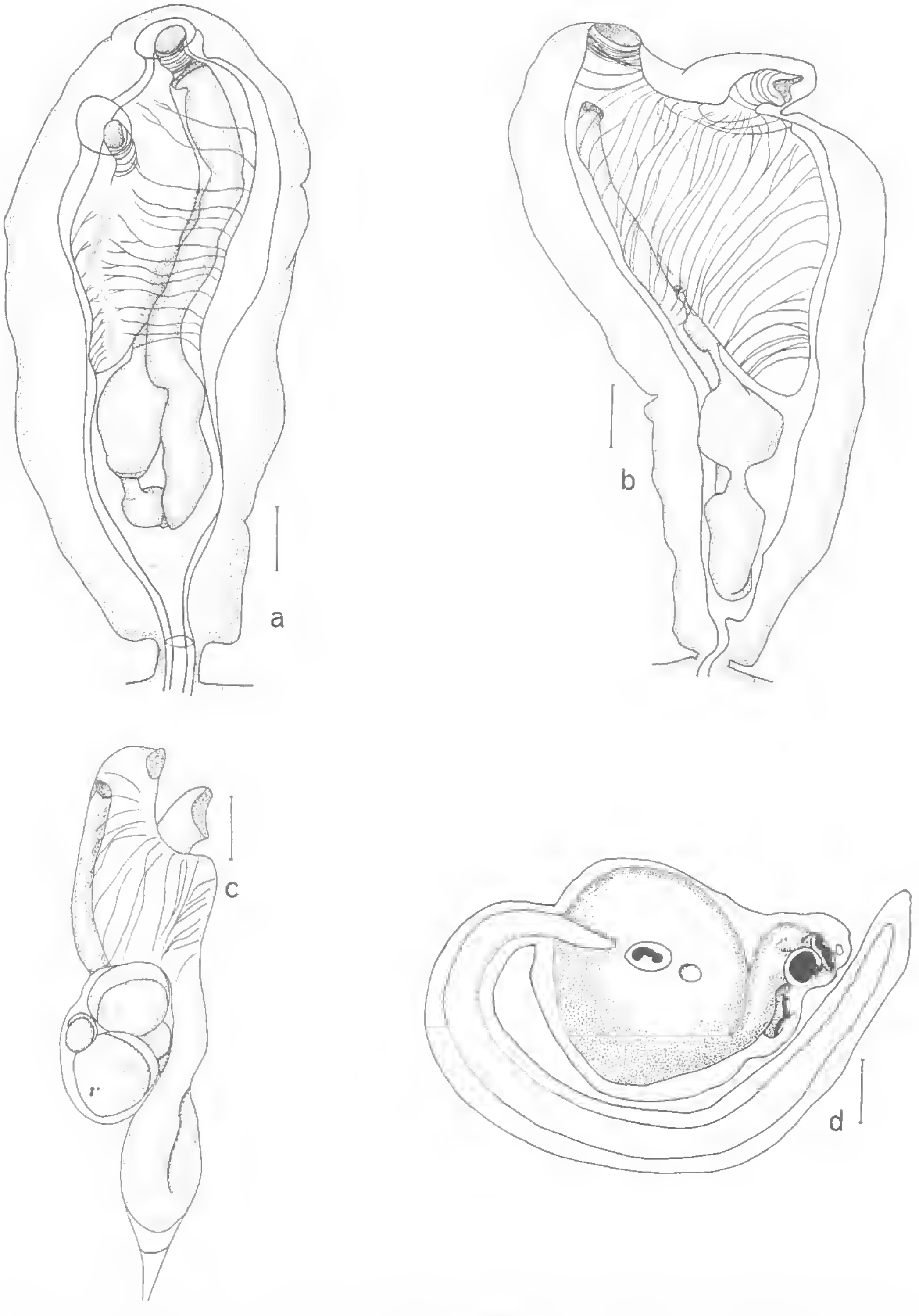


FIG. 10, *Clavelina cylindrica*: **a,b**, zooids from left and right respectively showing test constriction where zooid attaches to common stalk (WAM 581.2.1, QM GH4068); **c**, zooid showing brood pouch with embryos (AM Y1190); **d**, larva (SAM E1962). Scales: **a–c**, 1mm; **d**, 0.2mm.

Clavelina cylindrica; Michaelsen, 1930, p. 475.
Podoclavella cylindrica: Kott, 1957a, p. 91; 1972a, p. 5 (part, specimens from West I, Wright I.); 1976, p. 56 (part, specimen from Western Port). Millar, 1960, p. 64; 1963a, p. 716; 1966a, p. 364. **Not** Kott 1972b, p.167; 1975, p.1 (< *C. moluccensis*).
Podoclavella australis, Kott, 1957a, p. 93 (part, specimen from Port Denison).

Distribution

New Records: Western Australia (Shark Bay, WAM 761.83; Wookoora Station, WAM 823.83; Houtman's Abrolhos, WAM 762.83 193.87 194.88 223.88; off Dongara, WAM 763.83; Cockburn Sound, WAM 581,2.31 73.75 81.75 124.75 156.75 165.75 178.75 758–60.83 764.83 984.83, QM G9482; Shoalwater Bay, WAM 115.75; Mandurah WAM 85.75 867.86; Margaret River, 866.86; Albany, WAM 28.75). South Australia (Great Australian Bight, SAM E1985, QM GH1279 GH4151; Yorke Peninsula, SAM E1961; Spencer Gulf, QM GH4287–8 GH4396). Victoria (Waterloo Bay, QM GH1279; Portsea, QM GH4068; Bass Strait, MV F53291; Wilson's Promontory, MV F53362–5, Mallacoota Inlet, MV F53660; Balnarring Beach MV F53658). Tasmania (Bruny I., MV F53659, SAM E1962; southern Tasmania, TM D1922).

Previously Recorded: Western Australia (Cockburn Sound — Michaelsen 1930, Millar 1963a, AM Y1187 Y1190 Kott 1957a; Albany — Millar 1963a). South Australia (St Vincent Gulf — SAM E1986 Kott 1972a). Victoria (Bass Strait — MacDonald 1858; Port Phillip Bay — Millar 1963a, 1966a; Western Port Bay — Quoy and Gaimard 1834, Millar 1960, Kott 1976). Queensland (Bowen — AM Y1186 Kott 1957a).

The species is often taken in storm debris washed up on beaches. The record from Queensland is anomalous, extending the range of this otherwise temperate species into the tropics. It is possible that the specimen was floating free in the East Australian current. The greatest depth from which the species has been recorded is 7m in Bass Strait.

Description

External Appearance: The rope-like colonies of this species are distinctive, consisting of a long central stem (up to 60cm or more long and 2 to 4cm in diameter) with separate zooids crowded along its length. Occasionally colonies are found in which the central stalk is attached along part of its length (QM GH4068); and sometimes it is branched at the base to form holdfasts. Zooids are short (seldom more than 1.0 to 2.0cm long) and entirely free, separated from the central stem by a marked constriction through which the vascular stolon of each zooid passes. The colony is sometimes attached to the substrate (weed or rock) by the basal (thickest) part of the stalk. In life, the colony is opaque blue or blue-grey. Pigment patches in the median line, between the siphons and over the anterior end of the endostyle and the anus, sometimes persist in preserved material. In preservative the zooids are often blue and the test is always translucent.

Internal Structure: The thorax is longer than the abdomen. However, since muscles are confined to the thorax it is often contracted in the preserved material, and thorax and abdomen are about equal length. The thoracic muscle formula is 10E,10B,4D. Although the endostylar muscles do not extend onto the abdomen, they do extend to the end of the thorax rather than the dorsal surface. They are oblique rather than transverse. Consequently their contraction both shortens the thorax and tends to draw down the ventral surface relative to the atrial siphon. Both siphons are rather wide with circular muscles around them and are often flaring and trumpet shaped.

About 24 sickle shaped branchial tentacles are present. The transverse vessels expand into relatively short and pointed dorsal languets over the dorsal sinus. There are from 9 to 13 rows of 50 to 60 stigmata. A small, rounded prestomach lies about halfway down the relatively short oesophagus. The stomach is a short oval halfway down the abdomen and there is also a large oval posterior stomach in the descending limb of the gut loop. The rectum extends almost from the pole of the gut loop at the posterior end of the abdomen to the base of the atrial siphon. The anal border is smooth.

Gonads are present in the gut loop, the small pear-shaped male follicles spilling over around the outside of the loop on the left side of the abdomen. A large brood pouch, formed by the expansion of the oviduct at the postero-dorsal end of the left side of the thorax, contains developing embryos, seldom more than 10, all at very different stages of development. Some have larval organs fully developed and others about half the size are without obvious development of organs. It is probable that fertilisation occurs in the brood pouch.

Embryos are present in the brood pouch in April, November and January from Shark Bay and Cockburn Sound (WAM 73.75 758.83 761.83 764.83 984.83); in September from Albany (WAM 28.75); in October from Western Port Bay (NMV F53658); and in November from southern Tasmania (TM D1922). However, they are not always present at these times from these locations. Only few specimens have been taken from May to August and these have no larvae. From present data, the species appears to breed from spring through to the following autumn.

Larvae are large and almost spherical, the trunk about 1.2mm diameter. They have 3 adhesive organs, triradially arranged and arising from a flat frontal plate that is not expanded into lobes. The adhesive organs consist of a shallow cup of differentiated epidermal cells around a broad, shallow axial cone. In the early embryo, the tail is wound vertically around the median line of the larval trunk with two adhesive organs and the cerebral vesicle just to its left, and the third adhesive organ to the right. As the larva develops the tail passes horizontally across the anterior end of the larval trunk from left to right, the two adhesive organs on the left moving up to the top and the one on the left moving to the ventral part of the anterior end of the trunk. The tail is long, almost completely encircling the trunk. The perforation in the larval test over each axial cone is conspicuous in this species.

Remarks: Kott (1957a) and Millar (1960, 1963a and 1966a) have suggested that this species and *C. australis* are conspecific. In fact, although both have zooids with large, robust thoraces and pigment patches in the median line, there are many distinguishing features.

Clavelina cylindrica invariably has short zooids, with an especially short abdomen arranged around a central common stalk; the zooids are always entirely free of the common test, from which they are separated by a sharp constriction; they have a prestomach in a relatively short oesophageal region; their thoracic muscles do not extend onto the abdomen; and they have an almost spherical larva and a rounded brood pouch. *Clavelina australis* has long zooids with a long oesophageal neck and no prestomach. Zooids arise from a basal mat or stalk from which they are never separated by a constriction and in which they are sometimes partially embedded. Their thoracic muscles extend the whole length of the thorax. Their larva is long, and their brood pouch is elongate, lying across the posterior end of the thorax.

Kott (1972a) confused *C. cylindrica* with *C. moluccensis*, as neither have abdominal muscles and both have a prestomach and rounded brood pouch. Again the constriction at the base of each separate zooid where it joins the central stalk distinguishes *C. cylindrica*, as does the pattern of its median pigment patches, the course of its thoracic muscles and its smaller larvae.

Clavelina dagysa (Kott, 1957)

(Fig. 11, Plate 3a)

Podoclavella dagysa Kott, 1957a, p. 93.

Distribution

New Records: Western Australia (Geographe Bay, WAM 4.75 121.75, QM G9485)

Previously Recorded: Western Australia (Rottnest I. – syntypes AM Y1188, AM Y1189 Y1191 Kott 1957a).

The species appears indigenous to the Western Australian coast – from Cape Naturaliste to Rottnest I. The maximum recorded depth is 20m.

Description

External Appearance: The species is relatively large (up to 4cm long) with a wide (up to 1cm) thorax and a slightly narrower cylindrical

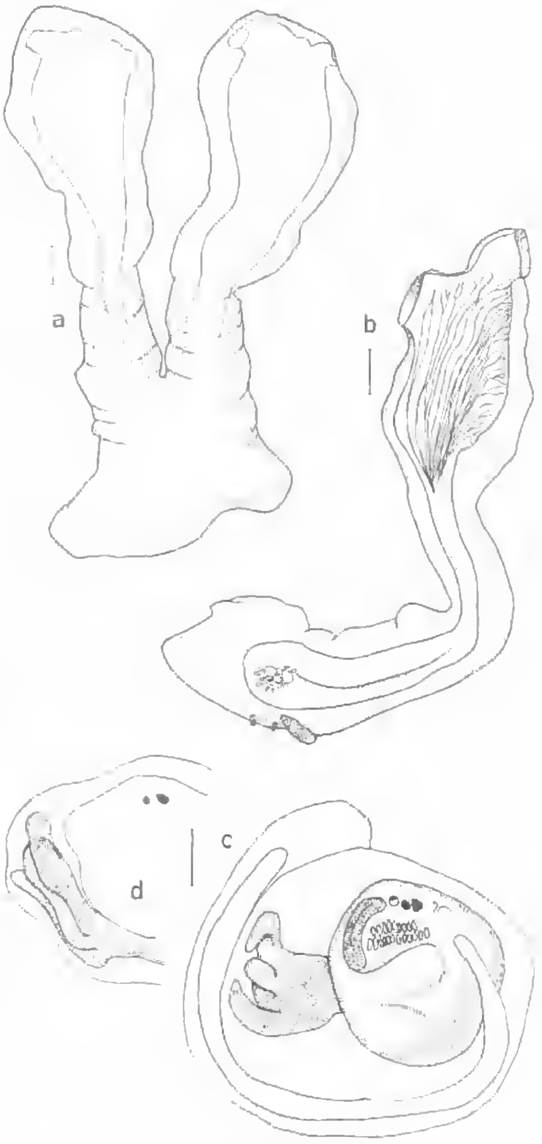


Fig. 11. *Clavelina dagysa*: **a**, colony (WAM 121.75); **b**, solitary individual (syntype AM Y1189); **c**,**d**, larvae showing adhesive organ from above, and from the left side (syntype AM Y1188). Scales: **a**,**b**, 2mm; **c**,**d**, 0.2mm.

stalk, rounded basally where it is fixed in sand and rubble. One specimen has been taken (AM Y1191) in which two zooids are joined basally, the posterior expanded portions of their abdomina being embedded in common test. The test over the thorax is always soft and glassy, while that of the abdominal stalk is firm, with sand and shell particles attached posteriorly. The zooid extends down into the base of the stalk and the vascular appendages are short. The apertures, on short siphons, are large, and flared when they are expanded. The branchial aperture is turned postero-ventrally and the atrial turned postero-dorsally. In life the zooid is uniformly blue and this colour remains in preservative.

INTERNAL STRUCTURE: Zooids are long, the thorax wide and roomy, joined by a narrow oesophageal neck of variable length to the posterior expanded part of the abdomen containing the stomach, gut loop, gonads and heart. The thorax is from half to one-third of the total length of the zooid. The thoracic muscle formula is +20E,3B,3D. The muscles extend along the whole length of the abdomen.

There are 8 robust branchial tentacles alternating with 8 smaller ones in a circle just anterior to the larger ones. These all alternate with rudimentary tentacles attached to the underside of a branchial velum projecting slightly into the base of the branchial siphon. The duct of the neural gland protrudes into the pharynx and has a curved or straight vertical opening. The dorsal languets are large triangular expansions of the transverse membranes over the dorsal sinus. Stigmata are in 24 to 30 rows of about 100.

The long oesophagus extends without interruption to the stomach in the posterior end of the abdomen. There is no prestomach. The stomach itself is oval, with a suture line, but although the stomach collapses into folds there is no sign of any structural folds or ridges. The rectum extends the whole length of the long abdomen and projects a short way up the thorax, the anus opening into the atrial cavity in the vicinity of the fourth last row of stigmata. The anal border has about 20 lobes. The gonads are, as usual, in the gut loop. They consist of pear-shaped male follicles surrounding the ovary and spreading over the left side of the gut loop. There is no brood pouch and embryos develop in the peribranchial cavity. They are present in colonies collected in November.

Larvae are large, the trunk being 1.3mm long with the tail wound three-quarters of the distance around it. They have an ocellus and an otolith. The frontal plate, supported as usual by a stolon from the abdominal part of the incipient adult, is flattened. However, the usual clavelinid adhesive organs are not present. Instead, each side of the frontal plate is extended into an arc of differentiated epidermal cells that may have an adhesive function. These two arcs enclose the slightly convex central part of the frontal plate.

REMARKS: A colony of *C. dagysa* consisting of 2 zooids, their abdomina embedded in a common stalk is recorded above. This provides evidence that this species, and probably *C. ostrearium*, replicate from terminal ampullae of the vascular stolon as in all clavelinids. As in *C. miniata* Watanabe and Tokioka, 1973, from Japan, replicated zooids probably separate from one another to become solitary.

Clavelina dagysa shares many of its principal characteristics with the southern Australian *C. ostrearium*. Both species have wide, roomy thoraces with oblique muscle bands dominating the musculature; long zooids with long oesophageal necks, and the posterior end of the abdomen expanding in the base of the stalk; short vascular stolons; zooids of the same uniform blue colour; and the thoracic test glassy and balloon-like, sharply differentiated from the test of the stalk. Both species have the posterior end of the stalk expanded, but in *C. dagysa* it is not hard and leathery and does not form a conical holdfast as it does in *C. ostrearium*. The species are convincingly separated by their larvae, which in *C. dagysa* do not have the usual clavelinid adhesive organs while in *C. ostrearium* they do. The range of these two indigenous species does not overlap — *C. dagysa* not being recorded south of Geographe Bay and *C. ostrearium* not being recorded west of Albany. However, they do not appear to be sister species. Another large and apparently solitary species, *Clavelina brasiliensis* (Millar, 1977) from the Brazilian Shelf, has the same modified frontal larval plate as *C. dagysa*, suggesting that it may be a plesiomorphic character inherited from some common ancestor rather than being associated with the isolation and speciation of the latter species in Australian waters.

The other large, solitary species commonly found in Australian waters, *Clavelina meridionalis*, is tropical and is not recorded south of Houtman's Abrolhos on the Western Australian coast. It is distinguished from both *C. dagysa* and *C. ostrearium* by its long thorax, more numerous thoracic muscle bands, relatively short zooids, long vascular stolon, and the absence of the blue pigmentation so characteristic of the present species and its South Australian relative.

Clavelina fecunda (Sluiter, 1904)
(Fig. 12)

Podoclavella fecunda Sluiter, 1904, p. 7.
Clavelina fecunda: Tokioka, 1967a, p. 101. Monniot, 1988, p. 203.

DISTRIBUTION.

NEW RECORDS. Western Australia (Rottnest I.). Queensland (Heron I, QM GH4075–77 GH4086; Lizard I., GH4110–1 GH4114–7). Philippines (QM GH405–6 GH474). Northern Territory (Stephen's Rock, QM GH4697).

PREVIOUSLY RECORDED. New Caledonia (Monniot 1988). Indonesia (Sluiter 1904). Palau Is (Tokioka 1967a).

The species appears to be a tropical western Pacific one, recorded from shallow intertidal waters down to 20m in coral reef habitats.

DESCRIPTION

EXTERNAL APPEARANCE. Despite their small size (about 1cm long) the zooids are conspicuous amongst the cryptofauna because of their bright colour, having yellow patches each side of the

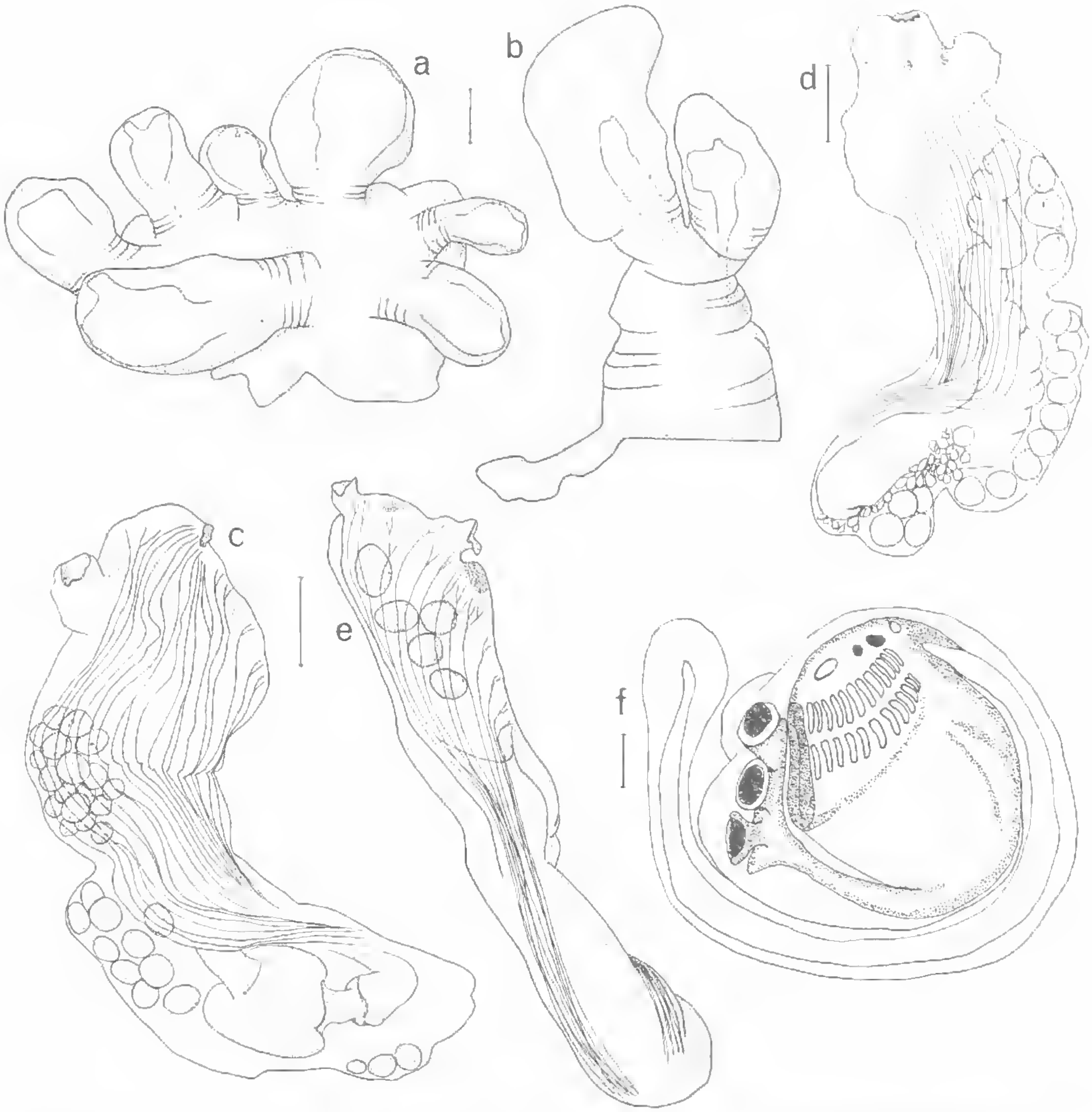


FIG. 12, *Clavelina fecunda*: **a,b**, colony (QM GH4077 and from Rottnest I.); **c,d**, zooids showing numerous eggs and incubating embryos in distal part of oviduct (QM GH4075); **e**, zooid (Rottnest I.); **f**, larva (QM GH4075). Scales: **a,b**, 2mm; **c–e**, 1mm; **f**, 0.1mm.

thorax, blue in large patches over the endostyle, between the siphons and spreading around the atrial siphon and over the dorsal lamina, and two lighter blue patches on each side of the thorax. In preservative the zooids become uniformly dark blue.

One solitary zooid was taken, but its basal test was crowded with masses of terminal ampullae. A colony consists of up to 10 crowded zooids arising from a basal mass of common test in which the abdomina of the zooids are partially embedded. The thoracic test is clear and glassy while the lower stalk-like section of the free part of each zooid, and the basal test are firm and translucent. Zooids are up to 1cm long and the expanded thoraces up to 0.5cm wide.

INTERNAL STRUCTURE: The thorax is about one third of the length of the zooid, with its branchial aperture turned ventrally and the atrial aperture directed upwards. The thoracic muscle formula is 7E,5B,3D, and all the muscles extend to the posterior end of the abdomen. Sometimes the ventral oblique muscles are obscure. There are 6 large branchial tentacles alternating with smaller ones. The opening of the neural gland is a vertical slit.

There are 16 to 20 rows of about 50 stigmata. The oesophageal section of the zooid is moderately long. There is no prestomach. The stomach, in the posterior end of the abdomen, is quadrilateral in section, and curves around against the mesial wall of the intestine. It has a fine ridge enclosing, with the suture line, a pear shaped area on its outer wall. A rounded posterior stomach lies almost in the pole of the gut loop. The proximal part of the rectum is voluminous and yellow. The smooth, bilabiate anal opening is at the posterior end of the thorax.

In mature specimens the gonads, in the loop of the gut, are conspicuous, the testis follicles spilling out over the left side of the gut loop. Large eggs are numerous and fill the whole length of the oviduct, apparently beginning their development in the terminal, expanded part of the oviduct, which forms a brood pouch — although this does not markedly protrude outside the wall of the thorax.

Embryos and larvae are present in the newly recorded specimens from Heron I. collected in late October and early November. They are also present in some of the specimens from Lizard I. which were all collected in June. They are not present in specimen lot QM GH4117 also collected in June. Despite the large eggs, larvae are relatively small, the trunk being 0.75mm long with the tail wound about half way around it. Three adhesive organs lie on a flat frontal plate, each with a cup of epidermal cells around a central cone. The frontal plate is produced into small lobes between the adhesive organs.

REMARKS: Tokioka (1967a) remarked on the unusually fecund appearance of this species, and those newly recorded specimens that have embryos, are no exception. Other distinctive characters are the short, stumpy zooids, and the bright yellow colour in the living specimens. Philippine specimens (QM GH474) are the same colour as those recorded from Australia, described by the collector (M.E. Cowan) as 'transparent blue with yellow markings'. Colonies and zooids of the present species resemble those of *Clavelina elegans* (Oka, 1934) from Japan, and conspicuous morphological differences in the preserved material of *C. elegans* and *C. fecunda* have not been detected. In *C. elegans*, larvae have a longer (0.9mm) trunk, and larger zooids (2 to 3cm) than those of the present species, and yellow patches are not present in living specimens. *Clavelina obesa* has small stumpy zooids without yellow patches, joined by stolons rather than being partially embedded in common test as in the present species, and with transverse rather than longitudinal musculature.

Clavelina meridionalis (Herdman, 1891)

(Fig. 13, Plate 3b-d)

Podoclavella meridionalis Herdman 1891, p. 603; 1899, p.4. Hartmeyer, 1919, p. 104. Hastings, 1931, p. 81. Kott, 1957a, p. 91; 1972d, p. 241. Not Sluiter, 1895, p. 165 (< *C. robusta* n.sp.); Pizon, 1908, p. 197 (< *C. robusta* n.sp.); Kott, 1972b, p. 167 (< *C. ostrearium*).

Podoclavella procera Sluiter, 1904, p. 8.

Clavelina enormis: Kott, 1957a, p. 85.

DISTRIBUTION

NEW RECORDS: Western Australian (Dampier Archipelago, WAM 26.75; Monte Bello Is, WAM 749 50.83; Houtman's Abrolhos, WAM 747-8.83). New South Wales (Port Stephens, QM G10149, AM Y1999; Solitary Is, QM G9641). Queensland (Bowen, QM GH705 GH4080; Mackay, QM G4944 G9978).

PREVIOUSLY RECORDED: Western Australia (Port Charles — AM Y1159 Y1255 Kott 1957a; Cape Boileau, Cape Jaubert — Hartmeyer 1919). New South Wales (Port Stephens — AM U3936 Herdman 1899; Port Hacking — AM Y818 Kott 1972d; Port Jackson — holotype AM U113, AM G12247 Herdman 1899). Queensland (Mackay — AM Y1192 Kott 1957a; Low Is — Hastings 1931). Indonesia (Sluiter 1904).

The species is tropical, although its range on the eastern Australian coast extends into the subtropical waters of New South Wales. It has been taken at depths down to 20m.

Description

External Appearance: The species is large and solitary, up to 20cm long, consisting of a cylindrical thoracic section in translucent (but not glassy) test that is a half to one-third of the total length and is from 0.5 to 1cm wide when expanded. The stalk narrows from the posterior end of the thorax to its base, where it sometimes breaks into fine hair-like roots or occasionally branches off the stalk of another zooid (see AM Y1255), but most often is fixed directly to the substrate. As it narrows, the stalk becomes increasingly hard and leathery. In its upper part it contains the abdomen of the zooid but toward the base it contains the long vascular stolon. The large terminal branchial siphon is turned over with its opening directed toward the base of the zooid. The atrial siphon is directed upwards. Both siphons flare when they are expanded. In life the thorax is a transparent green with a yellow patch each side of the intersiphonal region and along the endostyle. Some photographs of this species show the test pink. In preservative the anterior part of the thorax, brood pouch and abdomen are dark blue to black, but the remainder of the thorax is cream to brownish cream.

Internal Structure: The zooid is robust but not very long. Thorax and abdomen together are about 3cm long in contracted specimens and even in living zooids are only about half the total length, the long vascular stolon occupying most of the stalk. The muscle formula is 25-30E,2B,2D. Dorsal branchial siphon muscles and the anterior two-thirds of the endostylar muscles extend more or less horizontally across the body to the dorsal surface where they turn posteriorly and extend as fine bands down onto the abdomen. There they are joined by the posterior endostylar muscles which are truly oblique, extending from the endostyle to the postero-dorsal corner of the thorax and onto the abdomen in a dorsal and ventral band. Branchial tentacles are arranged in 4 rows, the largest in the posterior row. The neural gland opening is a vertical slit between two fleshy, protuberant lips. Dorsal languets are long, pointed projections from the triangular expansion of the transverse vessels over the dorsal sinus. There are about 35 rows of 70 to 100 stigmata.

The oesophagus is moderately long, without a prestomach. The stomach (in the posterior end of the abdomen) has 3 longitudinal ridges as well as the suture line in its inner lining. Folds in the stomach wall of some specimens are, apparently, artefacts of preservation. The stomach is often stretched into a long, narrow oval, but in other specimens it is more expanded. The gut is often voluminous and filled with mud. The anal opening is about one-third of the distance from the posterior end of the thorax, and its border has about 10 rounded lobes. Gonads are present in the gut loop, spilling out over the left side of the intestine and the proximal part of the rectum. A brood pouch forms from the expansion of the distal end of the oviduct, which extends across the posterior end of the right side of the thorax. Developing embryos are present in specimens from northwestern Australia collected in September (AM Y1255) and in specimens from Bowen collected in March (QM GH705).

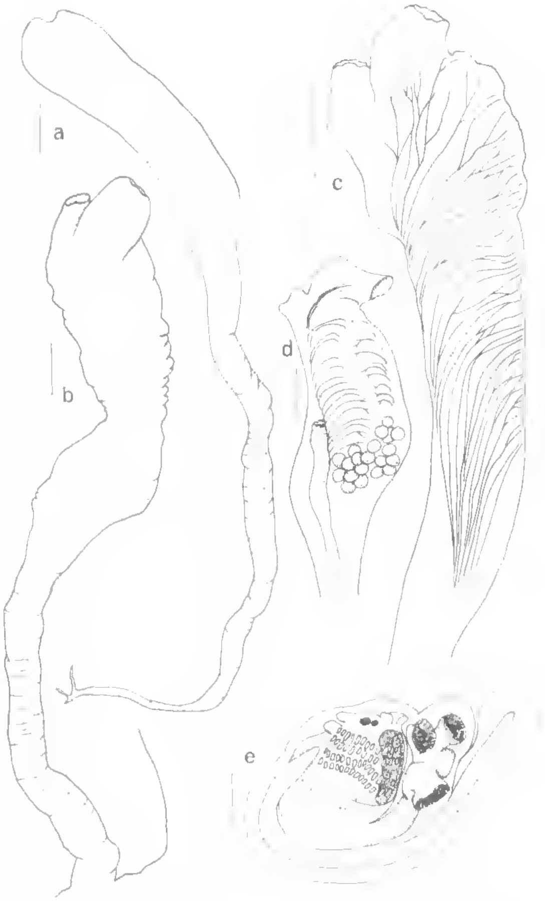


Fig. 13. *Clavelina meridionalis*: **a**,**b**, whole zooids (AM Y1255, QM G9641); **c**,**d**, thoraces removed from test, showing muscles, embryos brooding (AM Y1255, QM GH705); **e**, larva (AM Y1255). Scales: **a**,**b**, 5mm; **c**,**d**, 2mm; **e**, 0.2mm.

The larval trunk is 1.1mm long and the tail is wound only half way around the trunk. There is the usual frontal plate expanded into small lobes that alternate with the 3 adhesive organs triradially arranged.

The species is known to regenerate new zooids from old stalks (A. Birtles *pers. comm.*). The presence of a single zooid arising from the stalk of another suggests that occasionally replicates do develop before resorption of the adult zooid.

Remarks: Being solitary and of large size this species resembles *Clavelina dagysa* and the related species *C. ostrearium* from southern Australia. Like the latter species, *C. meridionalis* is known to regenerate new thoraces from persisting stalks; and like *C. dagysa*, it probably replicates zooids from the terminal ampullae of the vascular stolon. It is not known if zooids thus formed subsequently separate from the parent, as in *C. miniata* Watanabe and Tokioka, 1973. *Clavelina meridionalis* is isolated from both *C. dagysa* and *C. ostrearium* by its tropical range. The species is further distinguished by its larger number of transverse (endostylar) muscle bands, its long vascular stolon that occupies an appreciable part of the length of the stalk, its colour, and its smaller larvae. The brood pouch, extending across the posterior end of the thorax, resembles that of *C. australis* rather than that of *C. moluccensis* and *C. cylindrica*.

Kott (1972b), overlooking other differences, misidentified specimens of *C. ostrearium* as *C. meridionalis* on the basis of its solitary condition. *Podoclavella procera* Sluiter, 1904 resembles the present species in all respects, Sluiter even having recorded the fact that the musculature on the thorax was largely transverse.

Clavelina mirabilis Kott, 1972
(Fig. 14)

Clavelina mirabilis Kott, 1972b, p.165.

Distribution

New Records: None.

Previously Recorded: South Australia (Waldegrave I. — holotype SAM E902, paratype SAM E903 Kott 1972b).

The species is taken at 23m in gravelly sand. So far it is known from only a single location in the Great Australian Bight.

Description

External Appearance: Colonies consist of a wide, wrinkled cylindrical trunk rising vertically from a spherical sand-covered base (2 to 5cm in diameter) that is probably buried in the substrate. The trunk divides into branches each supporting a group of long zooids, their thoraces projecting separately from one another. The test is soft throughout, the spherical basal portion being protected by its brittle sandy outer layer.

Living specimens are buff or yellow-brown but in preservative the firm test of the stalk is reddish-

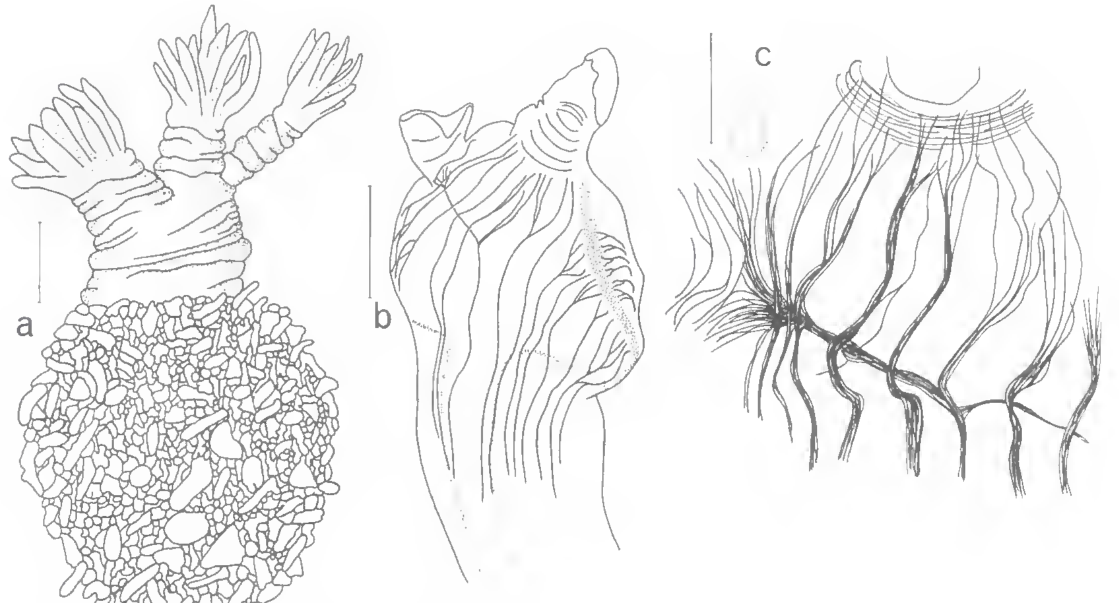


Fig. 14, *Clavelina mirabilis* (paratype SAM E903): a, colony; **b**, thorax, removed from test; **c**, antero-dorsal part of thorax showing muscle bands. Scales: a, 1cm; **b**, 1mm; **c**, 0.5mm.

purple, while the projecting thoraces are more or less transparent.

INTERNAL STRUCTURE: Zooids are long, up to 4cm. Each consists of a relatively short thorax and a long oesophageal neck that extends through the trunk of the colony and down into the spherical base where the rounded posterior part of the abdomen, the posterior vascular stolon and the terminal ampullae, are located. The musculature consists of oblique and longitudinal bands, with the formula 7E,8B,1D. The muscles extend along the length of the abdomen. An unusual transverse muscle originates as a branch from the sixth branchial muscle band about halfway down the thorax. It extends dorsally beneath other longitudinal muscles, with which it exchanges some fibres. At the base of the atrial siphon it breaks into narrow branches that join circular muscles of the atrial siphon. Branchial tentacles are in 3 rows, and the neural gland opening is simple and circular. There are 15 rows of about 45 stigmata per row. There is a long oesophageal neck, and the stomach, at the anterior end of a posterior expansion of the abdomen, is quadrilateral in section. Gonads of the usual type are in the loop of the gut posterior to the stomach. The larva of this species is not known.

REMARKS: The species resembles the new tropical species *Clavelina robusta* in its large, partially embedded zooids and in its musculature. However, *C. robusta* has an irregular branching basal stalk, or a massive basal test from which the zooids rise directly rather than extending through a branching vertical trunk that intervenes between the basal test mass and the zooid-bearing head. Colonies sometimes have a superficial resemblance to *C. pseudobaudinensis* which often has a similar massive basal test mass. Zooids of the latter species, however, are completely embedded, and the thoraces are not free as in the present species. The remarkable transverse muscle that crosses beneath the other longitudinal muscles from the centre of each side of the thorax to the base of the atrial siphon is reminiscent of *C. coerulea* Oka (see Nishikawa and Tokioka 1976) in which a muscle extends from the atrial siphon to cross the predominantly transverse thorax muscles. However, the course of this unusual muscle in *C. coerulea* is outside the transverse muscles, while in the present species the anomolous muscle runs inside the other predominantly longitudinal ones. The transverse muscle in the present species clearly originates as a branch from a longitudinal muscle and its formation could be through the mobilisation of fibres from the successive longitudinal muscle bands it crosses.

Clavelina moluccensis (Sluiter, 1904)

(Fig. 15. Plate 3e–h)

Clavelina (*Podoclavella*) *meridionalis* Sluiter, 1895, p. 165.

Podoclavella moluccensis Sluiter, 1904, p. 5. Kott 1957a, p. 90; 1972a, p. 5; 1972b, p. 167. **Not** Van Name, 1918, p. 130; Hastings, 1931, p. 82; Tokioka 1967a, p. 105; Millar 1975, p. 211; Tokioka and Nishikawa, 1976, p. 347 (all = *C. robusta* n.sp.)

Podoclavella cylindrica: Kott, 1972a, p. 5 (part, specimens from Hallet Cove); 1972b, p. 167; 1975, p. 1; 1976, p. 56 (part, specimens from Mallacoota Inlet).

The species name often is misspelt and even Sluiter (1904) used two different spellings. The name derives from the Moluccas, the Indonesian island group that is its type location.

DISTRIBUTION

NEW RECORDS: Western Australia (Exmouth Gulf, QM G9487; Houtman's Abrolhos, WAM 374.80; Shark Bay, WAM 757.83; off Dongara, WAM 756.83; Cockburn Sound, WAM 37.72 31.75 76.75 112.75 151.75, QM G9671; Bunbury, WAM 19.75; Albany, WAM 752.83 854.83). South Australia (Great Australian Bight, QM GH976, SAM E1988–9; Fleurieu Peninsula, SAM E1964; Nuyts Archipelago, SAM E1965; Yorke Peninsula, SAM E1966; St Vincent Gulf, SAM E1967–8, QM G9315 GH4066–7 GH4069–71, BM 1951.9.10.8; Kangaroo I., QM G11996). Victoria (Bass Strait, MV H376). Queensland (Heron I., QM G9517 G10041 G11913 GH359 GH4088; Lizard I., QM G9790; Martha Ridgeway Reef, QM GH246 GH543). Philippines (QM G12754 GH416 GH442–3 GH555). Singapore, ZMC 22.7.07.

PREVIOUSLY RECORDED: Western Australia (Cape Boileau — Sluiter 1885; Cockburn Sound — AM Y120 Kott 1957a; Hamelin Bay — AM Y1197 Kott 1957a. Albany — AM Y1199 Y1203). South Australia (Great Australian Bight — SAM E1963 Kott 1972b, SAM F2086 Kott 1975; Spencer Gulf — AM Y1198 Kott 1957a, SAM E1969–72 Kott 1972a, 1975; St Vincent Gulf — SAM E991 Kott 1972a). Victoria (Mallacoota Inlet — Kott 1976). Indonesia (Sluiter 1904).

Although there are no records from New South Wales, the species has been photographed there, at Jervis Bay and Port Stephens (photos P. Frederickson). This apparently is a tropical western Pacific species. It occurs quite commonly in the Philippines (see new records). It is seasonal in some locations (e.g. Tipara Reef: Shepherd *fide* Kott 1972a), dying off at the beginning of summer and reappearing in early winter. Apparently this is not always the case for there are records from Cockburn Sound for every month except May and records from the tropics include the winter months.

DESCRIPTION

EXTERNAL APPEARANCE: Large irregular colonies with single zooids or upright stalks support groups of zooids separated from one another to various degrees, from whole zooids to at least the thoraces separated. The test of the basal stolons

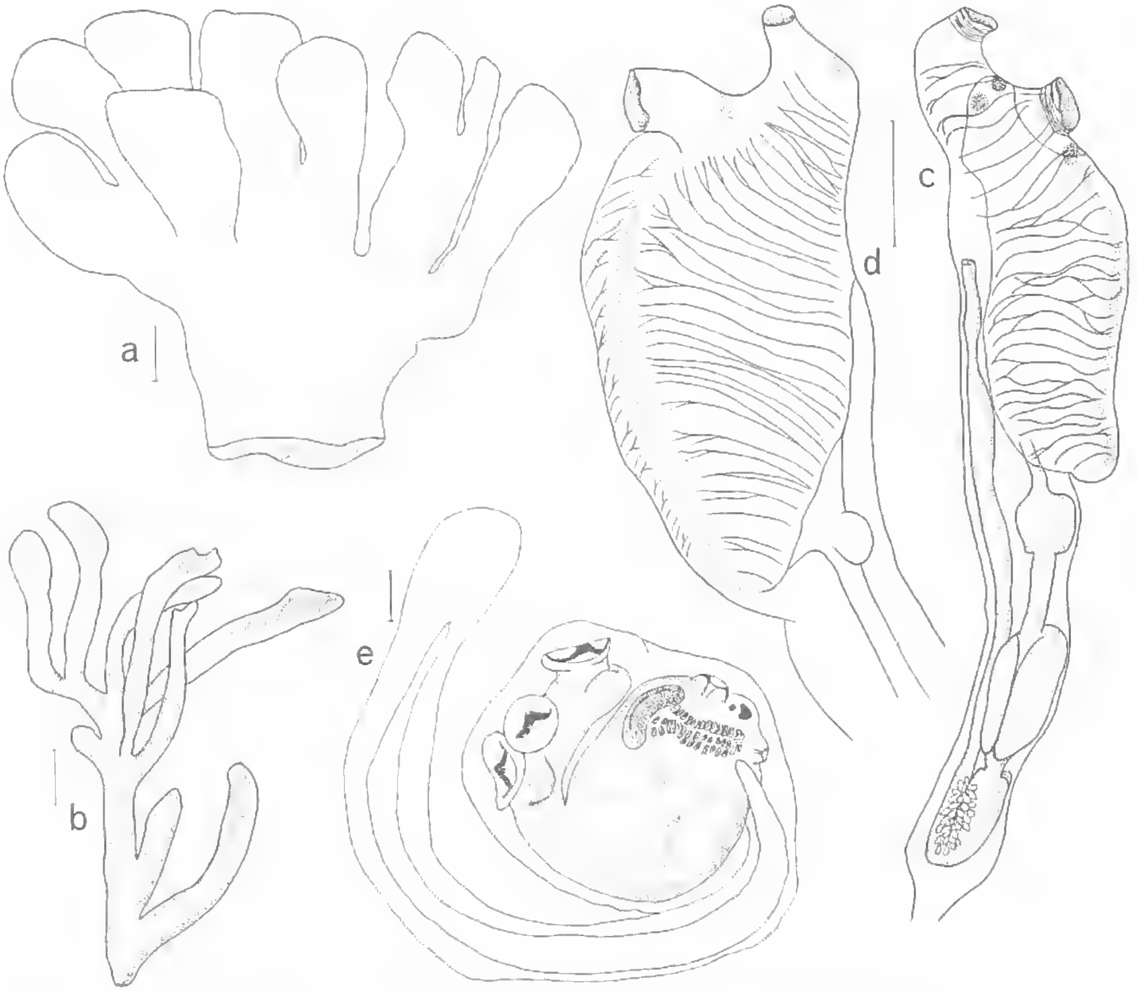


FIG. 15. *Clavelina moluccensis*: **a,b**, colonies (SAM E2086; WAM 854.83); **c**, zooid (QM GH 4070); **d**, thorax (WAM 854.83); **e**, larva (AM Y1196). Scales: **a,c,d**, 2mm; **b**, 1cm; **e**, 0.2mm).

or test mass and the lower part of the zooid-bearing lobes is firm and only slightly translucent, and the test over the thoraces is softer and more transparent, although it is not glassy. Sometimes the basal test develops into a thick stalk-like support for the colony and sometimes it forms fleshy stolons. The free, branched, zooid-bearing clumps or single zooids are from about 0.8 to nearly 3cm long.

Living zooids are blue, some pale, others darker, the colour conspicuous, showing through the transparent test. A characteristic pattern of patches of darker blue is always around the anterior end of the zooid. This consists of a transverse line of 3 blue spots between the siphons, a patch over the anterior end of the endostyle, another posterior to the base of the atrial siphon and a small spot over the anus. These patches of blue persist in preservative though zooids are often bluish-black.

INTERNAL STRUCTURE: Zooids are from 0.5cm to 2.5cm long. The thorax always longer than the abdomen and, in preserved specimens in which the muscles are contracted, it is no wider than the abdomen. The vascular stolon is long, a great part of it in the upright zooid-bearing stalks. Terminal ampullae of the vascular stolon are numerous, branching off along its whole length.

The apertures are on short siphons, the atrial usually terminal, turned slightly ventrally, and the branchial subterminal and curved ventrally and posteriorly. Thoracic muscle bands are all transverse, extending across the sides of the body to the dorsal border where they disappear. A few fine bands sometimes can sometimes be detected along the dorsal surface extending onto the abdomen, and, although these presumably are present always, they are inconspicuous and difficult to demonstrate in unstained material. The muscle formula is 20–30E,3B,3D. Contraction of the transverse thoracic muscles causes the thorax to become long and narrow.

There are about 24 branchial tentacles of varying size. The neural gland opening is elliptical, set vertically and slightly obliquely. From 14 to 22 rows of about 80 stigmata are in the branchial sac.

The oesophagus extends down the anterior one-third of the abdomen, interrupted about halfway along its length by a small rounded prestomach. The stomach is large and roomy. Generally its internal lining is interrupted only by the suture line, however, in a large specimen from St. Vincent Gulf (QM GH4066) there are also 3 fine ridges. A large posterior stomach occurs at the posterior end of the descending limb of the gut loop before it curves around and expands into the rectum, which occupies the whole of the ascending limb of the loop. The anal opening is about halfway up the thorax, its border smooth and bilabiate.

Gonads are of the usual form, located in the gut loop posterior to the stomach, and the pear-shaped male follicles spill out over the posterior end of the gut loop obscuring it. Eggs are relatively small. Developing embryos are present in a rounded brood pouch formed by the expansion of the distal end of the oviduct projecting from the postero-dorsal corner of the thorax. They continue their development in the peribranchial cavity. Embryos are present in colonies from Rottnest (WA) and Yorke Peninsula (SA) collected in October to December (WAM 11.275, AM Y1196, SAM E1966); and from Bass Strait in December (NMV H376); in one colony from the Fleurieu Peninsula (SA) taken in July (SAM E1964), and in colonies from Heron I. (QM G9517) in November. Young colonies were common at Heron I. in May 1988.

The larval trunk is 1.2mm long and is almost spherical. Adhesive organs are large, with the usual cup of modified epidermal cells around the central cone. They are supported by thick stalks arising from a broad frontal plate which is produced into conspicuous lobes between the adhesive organs. The tail winds completely around the trunk.

Remarks: Colonies of this species resemble those of *C. australis* and *C. robusta* n.sp.; and some of the larger specimens also have zooids of similar size. However, *C. moluccensis* can be distinguished readily by its transverse musculature, absence of conspicuous muscles on the abdomen, line of 3 pigment patches between the siphons (in addition to the median patches dorsal and ventral to the atrial and branchial siphons respectively) relatively short oesophageal neck, prestomach, rounded brood pouch, and a large larva with a long larval tail that completely encircles it.

Clavelina cylindrica has a similar brood pouch and prestomach but differs in its oblique and longitudinal muscles, even shorter abdomen and regular colony. *C. nigra* n.sp. has similar transverse muscles and prestomach but lacks the characteristic pigment patches. *C. coerulea* Oka also has similar transverse muscles but there are also longitudinal muscles, zooids narrow toward the base, and lack the prestomach.

Clavelina moluccensis does occur in the Philippines. However the records of Van Name (1918) and Millar (1975) from that location, as well as those of Hastings (1931) from Low Is, Tokioka (1967a) from the Palau Is, and Tokioka and Nishikawa (1976) from Japan, are not of this species. *Podoclavella moluccensis*: Van Name, 1918 includes numerous species (including one of the genus *Euherdmania*). It is unlikely that the present species is included, however, for all his specimens had predominantly longitudinal muscles that continue onto the abdomen. Some of Van Name's specimens probably are conspecific with *C. moluccensis*: Tokioka 1967a, *Podoclavella moluccensis*: Millar, 1975 and *C. moluccensis*: Tokioka and Nishikawa, 1976, which are all assigned to the new species, *Clavelina robusta* (see below).

Sluiter's (1895) description of this species includes a record of its characteristically spherical brood pouch (present even before it is filled with embryos), and its transverse muscles.

Clavelina nigra n sp

(Fig. 16, Plate 4a)

Distribution

Type Locality: Western Australia (Rottnest I., Roe Reef, 18m, coll. N. Coleman, AMP148, 6.3.72, holotype QM G9486).

Further Records: None.

Description

Colonies are irregular, consisting of thick basal stolons fixed to the substrate along their length, with upright branches containing single zooids or groups branching from a common stalk. Usually zooids are separate for most of their length although this is variable and occasionally only the

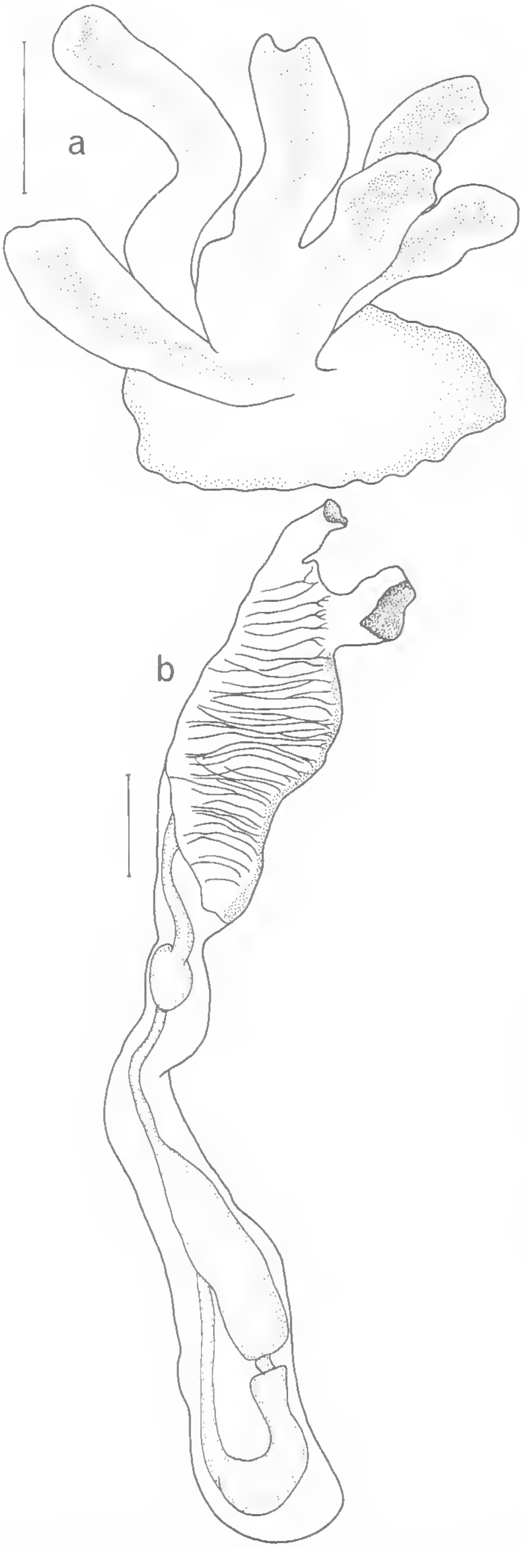


FIG. 16, *Clavelina nigra* n.sp. (holotype QM G9486): **a**, colony; **b**, zooid. Scales: **a**, 5mm; **b**, 1mm.

thoraces are separate. Separate zooids are up to 1cm long. The large subterminal branchial siphon is turned ventrally and the narrow atrial siphon is directed upwards, both flaring out from the aperture. Living specimens are dark grey to black with a white rim around each aperture. Even in preservative the body wall is crowded with dark particles.

INTERNAL STRUCTURE: The largest zooids are barely 1cm long and the thorax is slightly shorter than the abdomen. Thoracic muscle bands are transverse, with the formula 30E,4B,2D. Muscle bands are fine, forming an almost continuous coat over the thorax, but they disappear along the dorsal border and none were detected on the abdomen. Contraction of the thoracic muscles causes the thorax to elongate. Eight large branchial tentacles alternate with 8 smaller ones in a circle slightly anterior to them.

There are 19 rows each of about 50 stigmata. The oesophagus is interrupted by a small round prestomach about halfway along its length. A narrow oesophageal neck occupies half the length of the abdomen. The stomach is long, with a suture line, but no other folds or ridges. A long posterior stomach is present in the last quarter of the descending limb of the gut loop. The rectum extends the whole length of the abdomen and the smooth-bordered anus opens about halfway up the thorax. Gonads are present in the gut loop, but are not mature in this holotype colony.

REMARKS: The present species is strikingly similar to *C. moluccensis*. Both have transverse thoracic muscles, a prestomach, and similar, rather irregular, colonies with zooids arising singly or in clumps from common basal test or stolons. At least the thoraces, and sometimes the whole zooids, are separate from one another. Generally, the zooids are not as robust as *C. moluccensis*, the muscle bands are finer forming a continuous coat over the thorax, and are especially numerous for such small zooids. The abdomen is longer than the thorax in the present species, while it is shorter in *C. moluccensis*, and the numbers of stigmata per row are about half of the number in *C. moluccensis*. The most compelling difference between the two species, however, is the colour. The present species does not have the characteristic pigment patches of *C. moluccensis*, it is not blue, it has a white band around the apertures, and dark pigment particles are crowded throughout the preserved specimens.

The colour resembles that of *C. cyclus* Tokioka and Nishikawa, 1975 (see Nishikawa and Tokioka 1976) from Okinawa I. and the Philippines (QM GH475). However, the white band is around the base of the branchial siphon in *C. cyclus* — not around its rim as in the present species; and the thoracic muscles of *C. cyclus* are not transverse.

As far as is known, the present species occurs only at Rottnest I. It may be indigenous, with a range confined to Cockburn Sound.

Clavelina oliva n.sp.

(Fig. 17. Plate 4b)

Distribution

Type Locality: Western Australia (Shark Bay, Dirk Hartog I., Ransonnet Rocks, *Cymadocea* bed, coll. L Marsh 7.4.79, holotype WAM 983.83; Dampier Archipelago, Kendrew I., 20°28'30"S 116°32'E, outer metre 8, coll. Western Australian Museum Crown of Thorns Survey, paratypes WAM 217.75).

Further Records: Western Australia (Dampier Archipelago, WAM 213.7 thorax missing 1051.83; Houtman's Abrolhos, WAM 231.88). Queensland (Lindeman I., QM GH4085; Lizard I, QM GH4108). Northern Territory (Darwin, QM GH4211 GH 4800 1). Philippines (QM G12753 GH476 GH490 GH558).

Description

External Appearance: Specimens available are usually solitary, upright, club-shaped zooids on a narrow stalk which is divided into root-like branches at its base. The species is common (with *Nephtheis fascicularis*) in Darwin Harbour (at 13.5m) with its long stalk embedded in the silt and only the thorax rising above the level of the sea floor. Specimens have to be dug out of the substrate. The base of the stalk has often been severed. A colony with 4 zooids was collected from Lizard I. (QM GH4108). Another specimen lot (WAM 217.75) has 3 zooids that were possibly joined by a basal stolon, which could have remained attached to the substrate when the specimens were collected. Collectors field notes and photographs of the specimens from the Philippines (M.E. Cowan) indicate that the species occurs either in small colonies with few zooids or as solitary individuals.

The separate zooids are from 2.5 to 5.0cm long of which the thoracic, abdominal and posterior abdominal sections are each approximately one third. The abdominal section usually becomes progressively narrower with progressively firmer test toward the base, although sometimes the diameter decreases very abruptly to the narrow stalk at the posterior end of the abdomen. The thorax is about 8mm in diameter, abdomen about 5mm and narrow vascular stolon a maximum of only 2mm in diameter becoming narrower toward the base.

The test on the stalk is usually quite hard, leathery and opaque, although in all the specimens from Queensland it is firm and translucent, and sometimes is rather short. On the thorax the test is soft, flexible, and transparent, but not glassy.

In preservative the thorax is either transparent (specimens from Darwin), or dark blue, the colour fading toward the dorsal surface of the thorax and on the abdomen (specimens from Western Australia). Collectors notes and photographs of specimens from the Philippines indicate living specimens were dark (black?) with white, or yellow, or green bands around the siphons sometimes extending down the dorsal surface of the thorax and with speckles of the same colour on other parts of the thorax. In preservative some dark patches persist over the dorsal ganglion which extend around the base of the branchial siphon. However, in Darwin Harbour the populations of this species have a generally colourless thorax. The stalk and abdomen are yellow, and some yellow pigment extends up along the endostyle and around the apertures.

Internal Structure: The thorax is relatively large and roomy. The siphons are large, the branchial siphon curved ventrally and the atrial directed upwards. In addition to the usual endostylar, branchial and dorsal muscles, there are also conspicuous muscles from the atrial siphon extending down the dorsal surface. The muscle formula is 10E,5B,2D,4A. Endostylar muscles are spaced down the whole length of the endostyle. In contracted specimens muscles are seen to run transversely across the thorax, extending down the dorsal border of the thorax, onto the abdomen and along its length. In larger specimens 6 large branchial tentacles lie at the base of the branchial siphon, slightly anterior to them a circle of 12 of moderate length, and rudimentary tentacles are in the most anterior circle. However, in the small specimens from Lizard I. there is only a single circle of 9 rather short branchial tentacles. The opening of the neural gland is vertical, protruding slightly into the pharynx.

Stigmata and stigmatal rows both increase with body size, ranging from 11 to 22 rows of about 60 to 100 stigmata. When little contracted, the oesophageal neck occupies about half of the abdomen, the stomach being about half way down the abdomen. There is no prestomach. The stomach is large and wide, and sometimes has folds in the preserved specimens, although these are probably artefacts. The gut loop behind the stomach is obscured by gonads. The smooth-rimmed bilabiate anus opens at the posterior end of the thorax. Embryos are present in the distal part of the oviduct across the right side of the

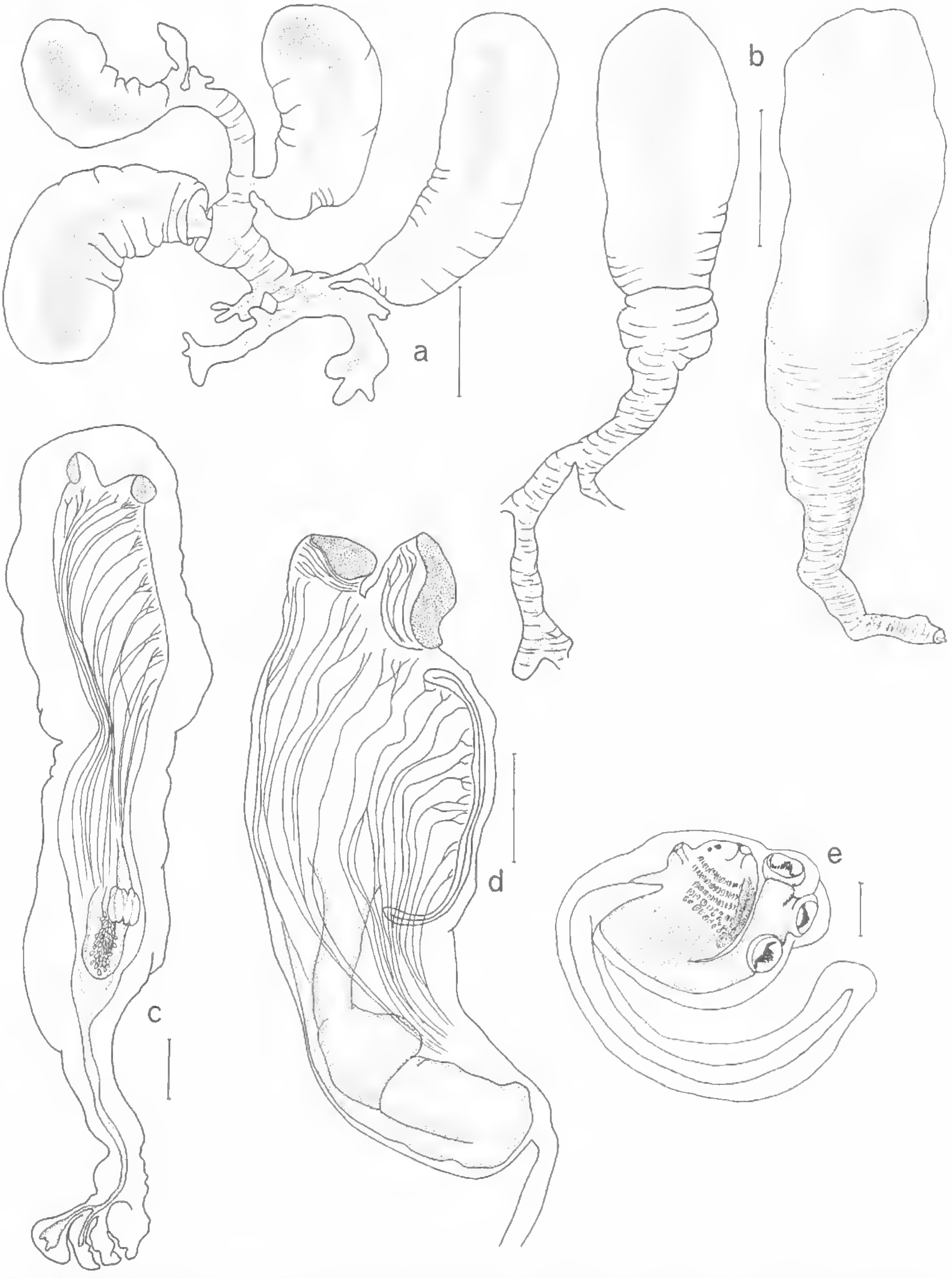


FIG. 17, *Clavelina oliva* n.sp.: **a**, colony (QM GH4108); **b**, solitary individuals (QM GH4108, WAM 1051.83); **c**, whole zooid in test (holotype WAM 983.83); **d**, zooid removed from test (QM GH4108); **e**, larva (QM GH4085). Scales; **a,b**, 5mm; **c**, 2mm; **d**, 1mm; **e**, 0.2mm.

posterior end of the thorax in specimens collected in February from the Dampier Archipelago (WAM 217.75), from Lindeman I. collected in January (QM GH4085) and from Darwin collected in August (QM GH4211).

A mature larva present in the specimen from Queensland (QM GH4085) has a trunk of 0.8mm to 1.0mm. The tail is wound more than halfway around the trunk. Although otolith and ocellus are present in the cerebral vesicle, these are not in good condition and the pigment appears lost. A rather narrow frontal plate has angular ampullae at the base of each adhesive organ.

REMARKS: The zooids of this species closely resemble those of *Clavelina viola* Tokioka and Nishikawa, 1976 from Sagami Bay, Japan. The holotype of the Japanese species is a large colony of 164 zooids, and this constitutes its major distinction from the present species which never forms large colonies. As indicated by the occurrence of some small colonies in the Philippines and the presence of enlarged terminal ampullae in one specimen from Shark Bay (WAM 983.83), it does sometimes replicate zooids from the basal stolon. However, replication seems not prolific; or perhaps, as in *C. miniata* Watanabe and Tokioka, 1973, replicates separate from one another.

The colour of the living zooids of *Clavelina viola* is recorded by Tokioka and Nishikawa (1976, p. 345)

> thorax . . . faintly purplish but darker near the posterior margin and in the siphonal area where a prominent deep purplish pigmentation is extending from the dorsal side of the atrial siphon onto each lateral side to embrace an area coloured yellow between both apertures.

Greater variation occurs in the colour pattern of *C. oliva*, with generally more yellow, white or green pigmentation in relation to the dark or purple areas. The inverted E-shaped dark patch over the dorsal ganglion that is considered a characteristic of *C. viola* is not present in *C. oliva*. Although longitudinal muscles from the atrial siphon have not been described for *C. viola*, they may have been overlooked and their presence in *C. oliva* does not necessarily constitute a difference between the species.

The characteristics that the zooids of *C. viola* share with the present species and that distinguish both from other species are: length of the zooids (3 to 4cm); their general shape, progressively narrowing from the thorax to the thin basal part of the stalk; long vascular stolon; general characteristics of the muscle formula, with a preponderance of oblique muscles; a relatively short oesophageal neck and the long posterior expanded section of the abdomen with its large roomy stomach that collapses into folds in preserved material.

Clavelina oliva is distinguished from the solitary *C. dagysa*, an indigenous Western Australian species not recorded north of Cockburn Sound, by its size; its attenuating basal stalk (the stalk of *C. dagysa* expands basally), its long narrow vascular stolon (instead of the short vascular appendages of *C. dagysa* in which the zooid extends almost to the base of the stalk); and its fewer muscles.

Clavelina ostrearium (Michaelsen, 1930)
(Fig. 18, Plate 4c)

Podoclavella ostrearium Michaelsen, 1930, p.467
Podoclavella meridionalis: Kott, 1972b, p.167.

DISTRIBUTION

NEW RECORDS: Western Australia (Albany, WAM 26.87). South Australia (Nuyts Archipelago, SAM E1973-4, QM GH2313; Pearson I., QM GH935; Great Australian Bight, QM GH936 GH4222).

PREVIOUSLY RECORDED: Western Australia (Albany — Michaelsen 1930). South Australia (Pearson I. SAM E1992 Kott 1972b).

The species occurs across the southern coast of Australia, mainly in the Great Australian Bight but extending into Oyster Harbour, Albany at its western limits. It has not been recorded inside Spencer or St Vincent Gulfs, however, and its presently known eastern limit is at Pearson I.

DESCRIPTION

EXTERNAL APPEARANCE: The species is solitary. Individuals are 6 to 11cm long, and consist of a spherical to oval balloon-like thoracic portion of glassy test enclosing a uniformly blue zooid, supported on a long firm, gelatinous stalk, wide in its upper part, and usually becoming leathery and tapering toward the base where it again expands into a tough conical hold fast or club-shaped, rounded base. The branchial aperture is terminal and the atrial aperture subterminal. Both apertures are on flaring siphons. The zooid extends right to the base of the stalk and the vascular stolon is very short. The expanded base contains the expanded posterior end of the abdomen.

INTERNAL STRUCTURE: The most conspicuous features of the zooid are the large (about 2cm long) roomy thorax and the long, thin oesophageal neck. Muscle bands of the thorax are longitudinal and oblique, with the formula 20E,10B,5D. They extend along each side of the abdomen. At the base of the branchial siphon 20 fairly large stumpy tentacles are in 3 concentric circles, with the larger tentacles in the posterior circle. The small tentacles

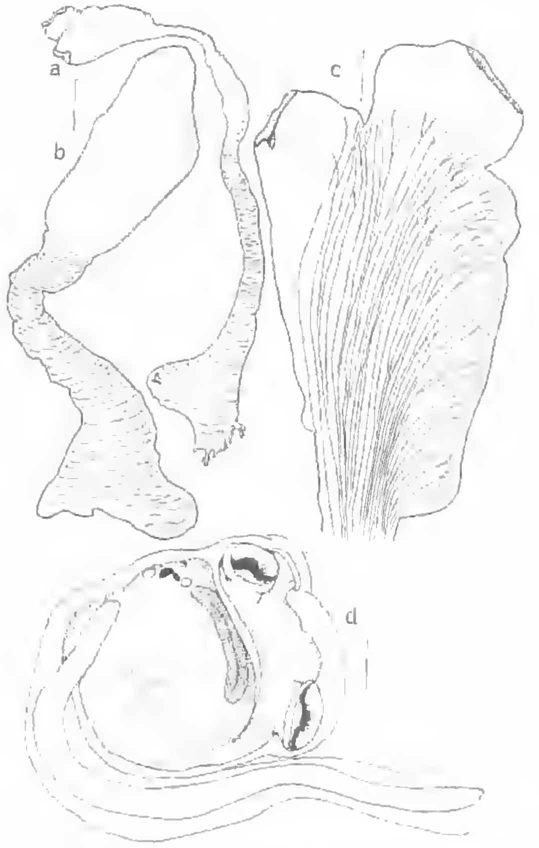


FIG. 18. *Clavelina ostrearium*: **a,b**, solitary individuals (QM GH2343, SAM E1973); **c**, thorax showing muscles (SAM E1973); **d**, larva (QM GH936). Scales: **a,b**, 5mm; **c**, 2mm; **d**, 0.2mm.

in the anterior circle are on the underside of a distinct velum that projects into the base of the siphon. The duct of the neural gland projects slightly into the pharynx and has a vertical elliptical opening, sometimes curved into an arc. There are 24 to 34 rows of at least 100 stigmata per row.

The long oesophagus extending through the greater part of the stalk of the zooid. It is not interrupted by a prestomach. The anus, its border divided into 20 rounded lobes, opens opposite the fourth last row of stigmata. The gut loop encloses the gonads, consisting of the usual central ovary surrounded by pear-shaped male follicles that spill over onto the side of the gut loop and obscure the long oval stomach and gut loop. Embryos develop in the distal part of the oviduct and in the peribranchial cavity but there is no protruding brood pouch. Embryos are present in colonies collected in March (QM GH936).

Larvae are moderately large, the almost spherical trunk being 1.25mm long. The frontal plate is broad and supports the usual 3 large triradially arranged, almost sessile adhesive organs. The tail is long, winding the whole way around the trunk. Shepherd (see Kott 1972b) observed that new thoraces regenerate on old persisting stalks. There is no evidence of vegetative replication in the examined material.

REMARKS. The species seems close to *Clavelina dagysa*, both being uniformly blue in life, and solitary with large, roomy thoraces, long oesophageal necks, short vascular appendages, and a similar muscle formula with predominantly oblique muscles. The stalk of *C. dagysa* usually is thicker and shorter, does not become as hard and leathery, and does not expand into a conical holdfast. However, the most compelling distinction between the two species is seen in the larvae – *C. ostrearium* has characteristic clavelinid adhesive organs while *C. dagysa* does not.

Michaelsen's (1930) specimen from Oyster Harbour, Albany, is described as 11cm long with a thin, leathery stalk, sharply cut off from the glassy thoracic portion which is about 2cm long, and has a short vascular stolon. Thus it conforms with all the characteristics of the present species.

Kott (1972b) mistook specimens of this species for *C. meridionalis*, which is also a tall solitary species with a leathery stalk. The latter species however, has a longer, narrower thorax, a shorter oesophageal neck, a long vascular stolon, and is a different colour.

Clavelina pseudobaudinensis (Kott, 1976)
(Fig. 19. Plate 4d f)

Oxycorynia pseudobaudinensis Kott, 1976, p. 54.
Clavelina baudinensis Kott, 1957a, p. 87 (part, not specimens from Rottnest with small larvae); 1972a, p. 4; 1972b, p. 167. ?Millar, 1966a, p. 363.
? *Synclavella lessoni* Caullery, 1900, p.1419.
? *Synclavella australis* Caullery, 1900, p.1420.

DISTRIBUTION

NEW RECORDS Western Australia (Houtman's Abrolhos, WAM 370.80; Cockburn Sound, WAM 745.83). South Australia (Spencer Gulf, QM GH4399 GH4401 2; St Vincent Gulf, QM G10118; Kangaroo I, QM G11992). Victoria (Port Phillip Bay, QM G9484 GH30). New South Wales (Jervis Bay, QM G10091; Wreck Bay, AM Y2001). Lord Howe I., (QM GH4375).

PREVIOUSLY RECORDED: Western Australia (Rottnest AM Y1112 paratypes *C. baudinensis* Kott, 1957a). South Australia (Great Australian Bight – SAM E1977 Kott 1972b; St Vincent Gulf SAM E1975 E1976 Kott 1972a). Victoria (Port Phillip Bay Millar 1966a; Western Port Bay AM Y1113 holotype, AM Y1122 paratypes Kott 1976).

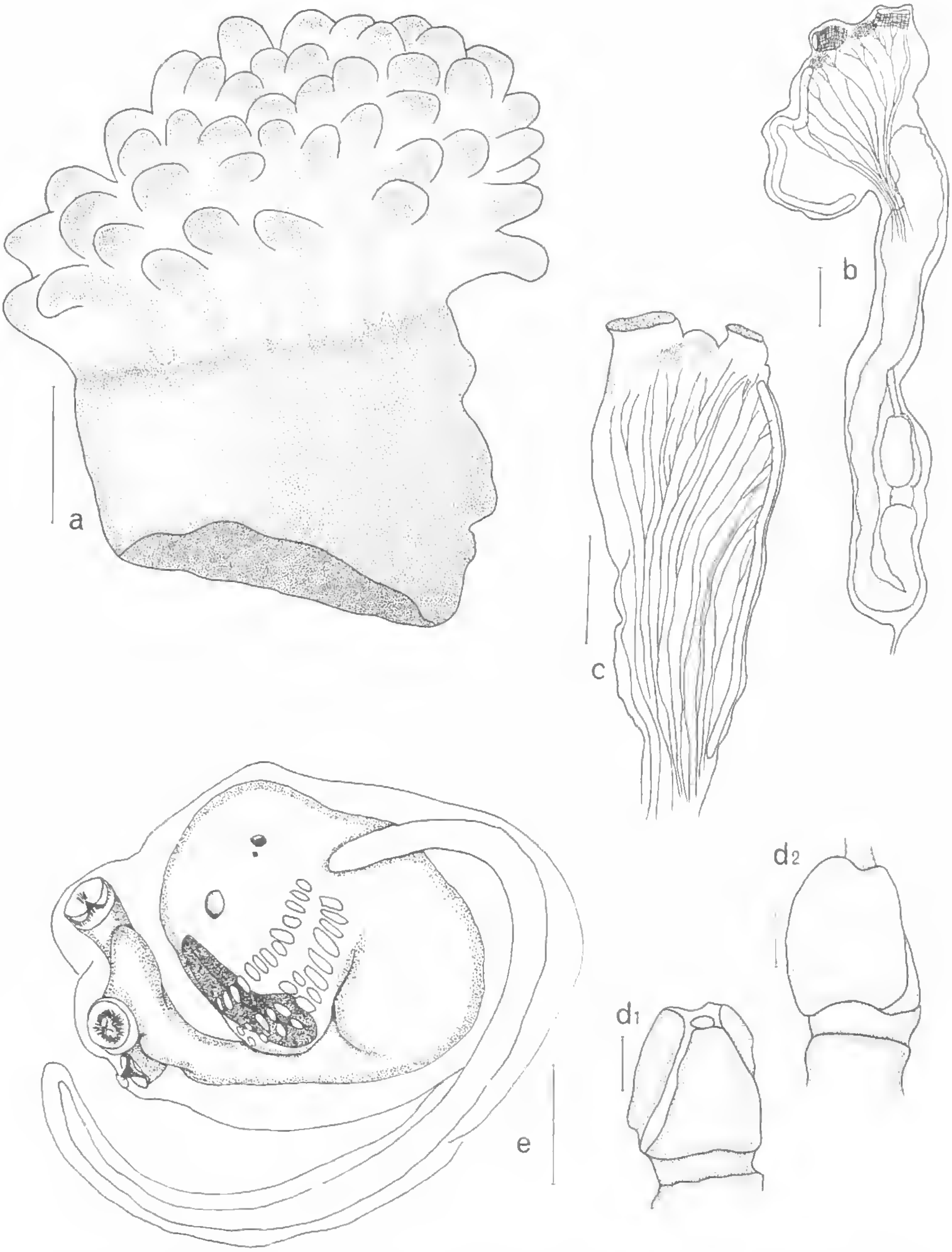


FIG. 19. *Clavelina pseudobaudinensis*: **a**, colony (SAM E1977); **b**, zooid (QM G11992); **c**, thorax (WAM 745.83); **d**, various views of the stomach (QM GH4072); **e**, larva (holotype AM Y1113). Scales: **a**, 5mm; **b,c**, 1mm; **d**, 0.25mm; **e**, 0.2mm.

The species has a wide range in temperate waters from Houtman's Abrolhos in Western Australia to Jervis Bay in New South Wales.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are mushroom-shaped, with a thick stalk and an almost spherical expanded head. The test is glassy and transparent on the upper surface where the zooids open. The stalk is firm, but not leathery. It is sometimes relatively long and narrow (up to 3cm long but less than 0.5cm diameter) with a head of 2cm diameter (AM Y1112 from Rottnest and QM G11992 from Kangaroo I.) However, more often the stalk is short, wide, sometimes bulhous and almost the same dimensions as the head. Zooids are almost completely embedded in the test, only their anterior ends projecting separately from the upper surface. The living specimens are transparent or grey with small white spots on the test and two conspicious blue pigment patches on the anterior end of each zooid — one a transverse arc between the siphons and the other a longitudinal patch over the anterior end of the endostyle. In darker specimens a horseshoe-shaped patch of white can be seen around the cerebral ganglion. The transverse arc of blue colour sometimes becomes either a large oval patch or separates out into 3 separate patches in the preserved specimens. There is also a small transverse patch of blue over the anus.

Blood vessels extend parallel to one another up toward the top of the stalk where they end blindly. Although vegetative buds were not observed it is possible that they develop here as they do in the genus *Nephtheis*.

INTERNAL STRUCTURE: Even partially relaxed zooids are not more than 1cm long, the thorax, the oesophageal neck and the posterior expanded part of the abdomen each being about one third of the total length.

Oblique and longitudinal muscle bands on the thorax have the formula 6E,3B,0D,3A. Sometimes muscle bands appear more numerous (up to 10E,6B,5A) when the thorax is not so strongly contracted and the separate bundles of fibres in each band separate from one another (see WAM 745.83, QM GH30). Branches from the adjacent branchial and atrial muscles extend across the inter-siphonal dorsal line. Muscles continue along the ventral side of the abdomen, and in many of the contracted zooids examined the abdomen is drawn up into a thick trunk behind the thorax (AM Y1112), or is folded up against the posterior end of the thorax, completely obscuring the oesophageal neck. Branchial tentacles are in 3 concentric circles, 6 large tentacles, at the base of the siphon, 12 moderately sized ones slightly anterior, and 12 small ones in front. The long, narrow, vertical opening of the neural gland projects into the pharynx.

There are 18 to 20 rows of 30 to 40 stigmata. Dorsal languets taper to a long, narrow point. The oesophagus is long and narrow in relaxed zooids, and there is no prestomach. The relativley short stomach is rectangular in outline, but apart from the suture line it has no structural ridges. Its mesial surface projects out at each side to embrace the intestine which it lies against. A long oval posterior stomach lies at the posterior end of the descending limb of the gut loop. The anus, bordered by rounded lobes, opens near the posterior end of the atrial cavity.

Embryos begin their development in the distal end of the oviduct, which forms a brood pouch, curving around from the oesophageal neck across the posterior end of the right side of the thorax. They complete development in the atrial cavity on the right side. Embryos are present in colonies collected from Rottnest I. in November (AM Y1112). In South Australian specimens collected in September (QM G10118) there are embryos developing in the brood pouch and atrial cavity, although tailed larvae are not present. Embryos and tailed larvae are present in the holotype colonies and in the specimen from Lord Howe I. (QM GH4375) collected in October. Specimens collected in March, April, June from South Australia and Victoria do not contain developing embryos. Apparently there is a single breeding season at the beginning of summer for this temperate species.

Larvae are large, the larval trunk 0.9cm long, with the tail wound five-sixths of the distance around it. The three triradially arranged stalked adhesive organs are supported on a frontal plate with small lobes produced from it to alternate with the adhesive organs. Each adhesive organ has a cup of modified ectodermal cells around the central axial cone. In one specimen (QM GH4375) the rows of stigmata in the larvae are actively subdividing and there are about 6 rather irregular rows.

REMARKS: Some colonies of this species (AM Y1112, QM G11992) closely resemble those of *Clavelina baudinensis*, having a fairly long and relatively narrow stalk. However, more often the stalk is short, wide and sometimes massive and bulbous. The zooids constitute a reliable means of distinguishing the species, for, while *C. baudinensis* never has oblique muscles, *C. pseudobaudinensis* has at least 5, extending from the anterior half of the endostyle. Also, the oesophageal neck of *C. pseudobaudinensis* is shorter, about the same length as the posterior expanded part of the abdomen, while in *C. baudinensis* it is two-thirds of the length of the abdomen. Living specimens can be distinguished by the transverse arc of blue pigment between the siphons. Further, *C. pseudobaudinensis* has a typically clavelinid larva, while the larvae of *C. baudinensis* are small and their adhesive apparatus is unique — not being known for any other species.

Clavelina pseudobaudinensis has a wide range in Australian temperate waters, while *C. baudinensis* is apparently confined to Cockburn Sound.

The two specimens referred to by Caullery (1900), on which he based the definition of the genus *Synclavella*, could be either the present species or *C. baudinensis*. However, since neither of the French expeditions which collected specimens, the *Coquille* and the *Astrolabe* respectively, visited Western Australian waters, Caullery's species are probably synonyms of *C. pseudobaudinensis*.

Possibly the species most closely resembling *C. pseudobaudinensis* is *C. australis* which, although they are not embedded completely, has large zooids, similar larvae, incubatory pouch and white spots in the test.

Clavelina robusta n.sp.

(Fig. 20. Plate 4g)

Podoclavella meridionalis: Pizon, 1908, p. 197.
Podoclavella moluccensis: ?Van Name, 1918, p. 130 (part). Hastings, 1931, p. 82. ?Millar, 1975, p.211.
Clavelina moluccensis: Tokioka, 1967a, p. 104. Tokioka and Nishikawa, 1976, p. 347.

Distribution:

Type Locality: Western Australia (Houtman's Abrolhos, Goss Passage, Beacon, Wallabi Group, 20–30m, coll. WA Museum party, 11.4.78, holotype WAM 753.83 *QM GH2140*; paratype WAM 755.83).

Further Records: Western Australia (Broome, WAM 751.83, QM GH2139; Exmouth Gulf, QM G11934; Shark Bay, WAM 754.83; Houtman's Abrolhos, WAM 374.80 230.88). Queensland (Lizard I., QM GH4073). Northern Territory (Port Essington, QM GH4074). Philippines (QM G12757).

Previously Recorded: Queensland (Low Is AM G13503 Hastings 1931). Palau Is (Tokioka 1967a). Indonesia (Pizon 1908). Philippines (?Van Name 1918, Millar 1975). Japan (Tokioka and Nishikawa 1976).

The species has a tropical western Pacific range.

Description:

External Appearance: Colonies are large, with large zooids, dark blue in preservative clearly seen through the whitish translucent test. In some zooids from which the colour is fading the blue pigment spreads around the sides from the dorsal surface and extends in a band along each side of the endostyle. It encloses a light coloured area over the anterior end of the zooid, and a dark patch down the dorsal surface of the branchial siphon. Collector's notes and photographs of Philippine specimens (QM G12757, coll. M.E. Cowan) indicate that living specimens were black with fluorescent green rings around the siphons, the ring around the branchial siphon being a wide band interrupted over the dorsal tubercle, while the ring around the atrial siphon is a narrow band around the rim of the aperture.

The basal part of the test is gelatinous and very firm, as is the test in the abdominal region. The test over the thoraces is softer and more transparent, but never glassy. Zooids are separate for varying parts of their length — sometimes the abdomen or some part of it is embedded in common test, or shares a stalk with another zooid, or often the whole zooid is entirely separate. The basal test often forms a massive or irregular stalk for the colony. Colonies are often solid, the zooid stalks adhering to one another.

Internal Structure: Zooids are large, 2cm to 4cm long with the thorax and posterior end of the abdomen about 0.5cm wide in fairly relaxed zooids. However, strong longitudinal muscles extend along the length of the thorax and abdomen and zooids are often strongly contracted. The posterior expanded part of the abdomen, containing the stomach and gonads, is about one quarter of the length of the more relaxed zooids. The remainder of the length is equally shared by the thorax and the oesophageal neck. Thoracic muscles are conspicuous and strong, with formula 8E,3B,3D. When contracted, muscles from the right side of the thorax swing around onto the ventral part of the oesophageal neck and then onto the left side of the posterior part of the abdomen. Muscles from the left side of the thorax curve dorsally and on to the right side of the abdomen. There are four large branchial tentacles in an outer circle and, anterior to these, an irregular arrangement of more numerous middle-sized and smaller tentacles. The opening of the neural gland is a vertical slit on a large fleshy cushion. There are 18 to 22 rows of 60 to 80 stigmata.

The oesophagus lacks a prestomach. The stomach is relatively narrow and pear-shaped, sometimes, but not always, with one or 2 ridges in the internal lining each side of the suture line. Gonads are in the gut loop. The ovary has particularly large eggs. Embryos are crowded, more or less in 3 rows in the upper half of the

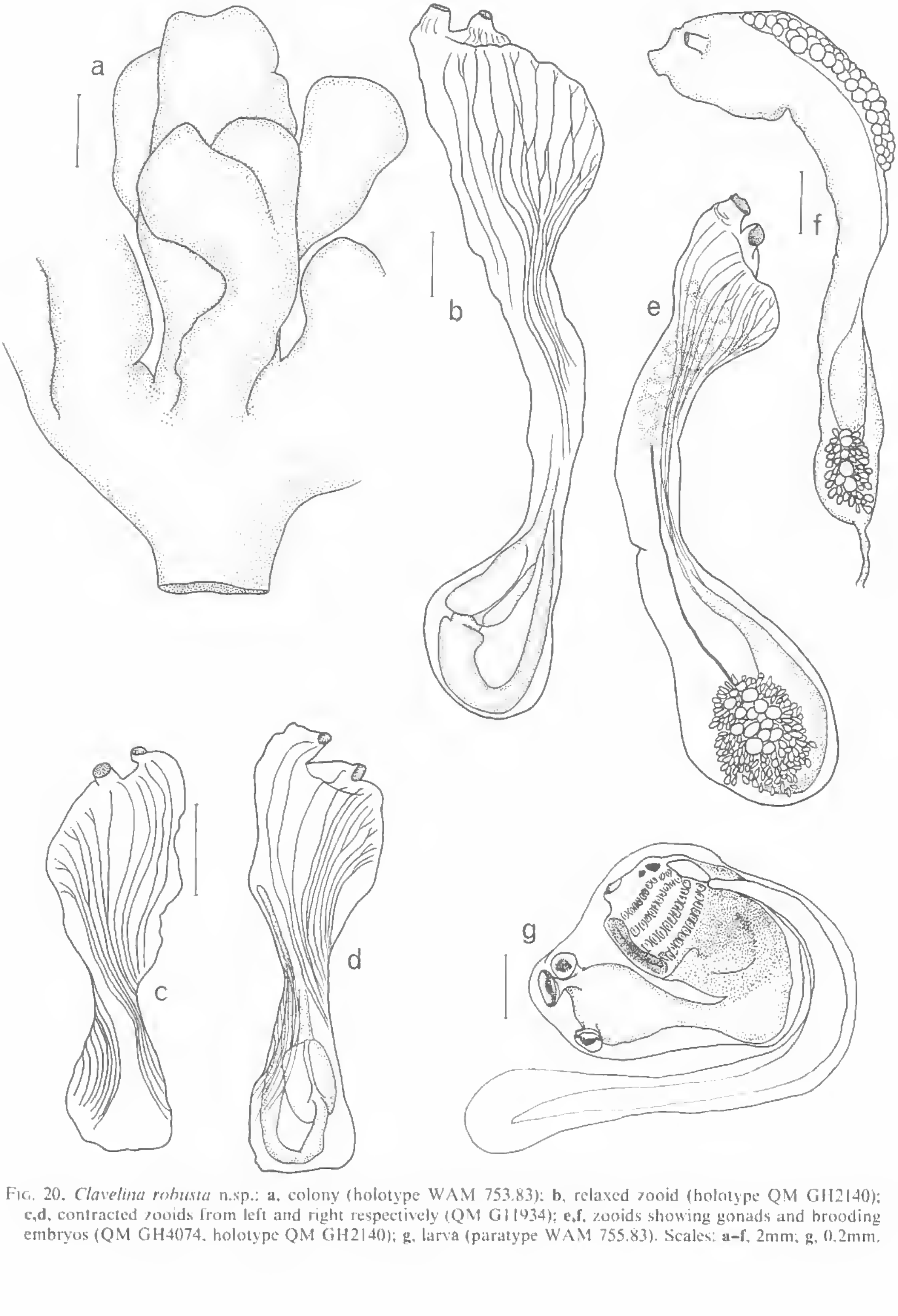


FIG. 20. *Clavelina robusta* n.sp.: **a**, colony (holotype WAM 753.83); **b**, relaxed zooid (holotype QM GH2140); **c,d**, contracted zooids from left and right respectively (QM G11934); **e,f**, zooids showing gonads and brooding embryos (QM GH4074, holotype QM GH2140); **g**, larva (paratype WAM 755.83). Scales: **a–f**, 2mm; **g**, 0.2mm.

oesophageal neck where the oviduct is expanded to form a brood pouch, where embryos begin their development, continuing it first in the distal end of the oviduct across the posterior end of the thorax and then free in the peribranchial cavity.

Larvae are large, the larval trunk being 1.3mm long. The tail is short, barely reaching the anterior end of the trunk. The 3 adhesive organs are well developed, with a relatively deep cup of ectodermal cells around the axial cone. The ventral stalk supporting the frontal plate is long, with small rounded ampullae alternating with the bases of the adhesive organs.

Embryos are present in colonies from Western Australia and the Northern Territory collected in September (QM G11934, GH4074) and from Western Australia in April (WAM 753–5.83).

REMARKS: The size of the zooids and colony, the long narrow oesophageal neck, and the muscle formula of this species are similar to *Clavelina australis*. The latter species can be distinguished by its median pigment patches, the absence of brooding embryos from the upper part of the oesophageal neck, as well as by its much smaller larvae with a relatively long tail. Certain aspects of the zooids and colonies resemble *C. elegans* which, however, has fewer oblique muscle bands and more longitudinal ones than does *C. robusta*.

The colour of the living specimens from the Philippines (QM G12757) closely resembles that of *Clavelina viola*. The latter species appears (from its photographs) similarly dark, with white, yellow or green spread over the thorax in speckles. In the present species this colour is confined to sharp bands around the siphons. Also *Clavelina robusta* zooids are more robust.

Clavelina moluccensis: Tokioka, 1967a and *Podoclavella moluccensis*: Millar, 1975 appear specimens of *Clavelina robusta* n.sp., having similar colonies, large zooids with a long oesophageal neck, a similar muscle formula, large larvae with small ampullae on the frontal plate, and a short tail. The branchial tentacles and dorsal tubercle of *C. robusta* are identical with those figured by Tokioka (1967a, fig. 35d). Further, the light area around the siphons in preserved specimens from Western Australia (WAM 755.83) is that part of the zooid which Tokioka describes as having been a very bright yellow colour in life. *Clavelina moluccensis*: Tokioka and Nishikawa, 1976 also appear specimens of *C. robusta* having, in addition to the other characters listed above, embryos in the upper abdominal part of the oviduct and purple pigment persisting in the anterior part of preserved zooids.

Genus **Nephtheis** Gould, 1856

Type species: *Oxycorynia fascicularis* Drasche, 1882

A monotypic genus of Clavelinidae with completely embedded zooids in a conical, fleshy, stalked head. The thick stalk contains a unique three-dimensional vascular network. Replicate zooids form in the terminal ampullae of this network. Unlike other Clavelinidae the terminal ampullae protrude from the vascular network at the top of the stalk just below the zooid-bearing part, rather than being distant from the zooids at the base of the stalk; and the ampullae do not separate from the vascular network prior to the development of the replicates.

There are no divisions of the gut posterior to the stomach although a prestomach is formed halfway down the oesophagus. The branchial tentacles are in a single circle on the edge of a narrow velum, and are not numerous. Larvae have the characteristic *Clavelina* form, being large with triradially arranged adhesive organs consisting of an axial cone of columnar cells surrounded by a collar of enlarged epidermal cells on a stalked frontal plate.

Nephtheis appears close to *Clavelina*. Zooids of *N. fascicularis* have muscles confined to the thorax as in *C. cylindrica*, as well as having the same short gut loop, prestomach, and long colony with zooids around the periphery of a central axial stalk (although in *C. cylindrica* the zooids are not completely embedded as they are in the present genus). Further, although the nephtheid meshwork vascular cylinder is not present in the genus *Clavelina*, in *C. pseudobaudinensis* the blood vessels do extend parallel to one another up the length of the stalk and terminate at the top as they do in the present genus. The principal distinctions between *Nephtheis* and *Clavelina* are the vascular network, and the single circle of branchial tentacles. Gonads of *Nephtheis* are smaller than those of *Clavelina*. Although testis follicles are larger, they are confined to the gut loop and are more or less in a circle around the ovary rather than spread around the outside of the gut as in *Clavelina*.

Nephtheis fascicularis (Drasche, 1882)
(Fig. 21, Plate 5a–c)

Nephtheis (?) Gould, 1856, p. 16.

Oxycorynia fascicularis Drasche, 1882, p. 175. Millar, 1963a, p. 717. Nishikawa, 1984, p. 116. Monniot, 1988, p. 205.

Nephtheis fascicularis: Tokioka, 1952, p. 100; 1970, p. 85. Millar, 1975, p. 209.

Colella thomsoni Herdman, 1886, p. 94.
Nephtheis thomsoni: Sluiter, 1909, p. 36. Hartmeyer, 1919, p. 121.
Nephtheis thompsoni: Van Name, 1918, p. 144.
Nephtheis malayensis Sluiter, 1909, p. 36.
Nephtheis faciformis Sluiter, 1909, p. 39.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, QM G9258, WAM 866.83 868.83 882.83). Queensland (Martha Ridgeway Reef, QM GH280 GH2093). Philippines (QM G12756 GH465 GH499). Northern Territory (Darwin Harbour). Australian coast (SAM F2037).

PREVIOUSLY RECORDED: Western Australia (North-western coast Millar 1963a). Arafura Sea (Tokioka 1952). New Caledonia (Monniot 1988). Ponape I. (Nishikawa 1984). Philippines and the Sulu Sea (Gould 1856, Van Name 1918, Tokioka 1970, Millar 1975). Caroline Is (Drasche 1882). Indonesia (Herdman 1886, Sluiter 1909).

DESCRIPTION

EXTERNAL APPEARANCE. Colonies have firm thick stalks, up to 3.5cm in diameter and 20cm long, although usually the stalk is in the vicinity of 2 to 3cm long. Sometimes many stalks are joined by common basal test, from which additional stalks arise. The diameter of the stalk usually decreases toward the zooid-bearing head. The heads are progressively spherical, conical, and long (up to 16cm) and cylindrical, the head lengthening as zooids are added from around the periphery of the vascular network at the top of the stalk. The largest specimen of the newly recorded material (WAM 866.83) is rope-like with a head 16cm long and the stalk 14cm. As ring after ring of zooids develop from the top of the stalk, the vascular network expands behind them, filling the centre of the head with an axis that is a continuation of the stalk, and that supports the lengthening head of the colony. Thus a conical to cylindrical head consists of an outer layer of zooids, their abdomina projecting inwards toward the vascular network of the central axis. Each zooid maintains its connection with the vascular network through its posterior abdominal stolon. Smaller heads consist of hemispheres to cones of zooids over the top of the stalk, their vascular stolons projecting down to join the vascular network that, at this stage, is confined to the stalk.

Several headless stalks are available from Roebuck Bay (QM G9258). These narrow to a point at their terminal free end. New zooids are developing around the narrowing free ends, the largest zooids at the top and the smallest further toward the wider base. These appear regenerating colonies in which the zooids have either regressed or have been lost through mechanical damage.

In the newly recorded material, long cylindrical and conical heads are from Roebuck Bay, Broome, while the specimens from the Great Barrier Reef and the Philippines are all shorter, spherical, oval or small cones.

The stalks are firm, although the vascular network confers on them a spongy texture. There is only a thin layer of test in the zooid layer of the head and it is exceptionally soft.

INTERNAL STRUCTURE. Zooids lie in the colony with their ventral sides toward the outside and the base. The branchial apertures are turned ventrally and open below the atrial apertures. Both apertures are smooth. Zooids are about 1cm long, the thorax longer than the abdomen. Thoracic musculature, with formula 24E,4B,4D,3A, consists of relatively short transverse and oblique bands extending across each side from the atrial siphon, the branchial siphon and the endostyle, and attenuating over the dorsal and posterior borders of the thorax. Muscles do not extend onto the abdomen. There are only 8 branchial tentacles, produced from the edge of a narrow velum. The opening of the neural duct is a simple oval opening.

Newly recorded colonies have from 12 to 14 rows of stigmata. Zooids at the top of the large heads from Roebuck Bay have 14 rows and those at the base of the same head have 12 rows of stigmata. Smaller colonies from Martha Ridgeway Reef have 13 rows in zooids at the top and 12 in those at the bottom of the heads. About 30 stigmata are in each row. The gut loop is short. A small rounded prestomach lies halfway down the oesophagus, and a rounded stomach, with a suture line but no other structural folds or ridges, is about halfway down the abdomen. No other structures differentiate any part of the gut, which continues as a plain cylindrical tube extending from the end of the stomach to the anus, (about halfway up the thorax). Gonads are confined to the pole of the gut loop posterior to the stomach. The central ovary, containing up to 8 large eggs, is surrounded by relatively large testis follicles. A small incipient brood pouch occurs at the postero-dorsal corner of the thorax.

Neither embryos nor larvae were present in the newly recorded specimens which were collected in May, July and October. Tokioka (1952) records up to 6 embryos in the brood pouch in specimens from the Arafura Sea in October. Larvae are large. The trunk 1mm long and deeper than long. The 3 adhesive organs are of the usual clavelinid type with a collar of cells around the central cone, and they are triradially arranged on a frontal plate (see Tokioka 1952).

REMARKS. In the newly recorded material the

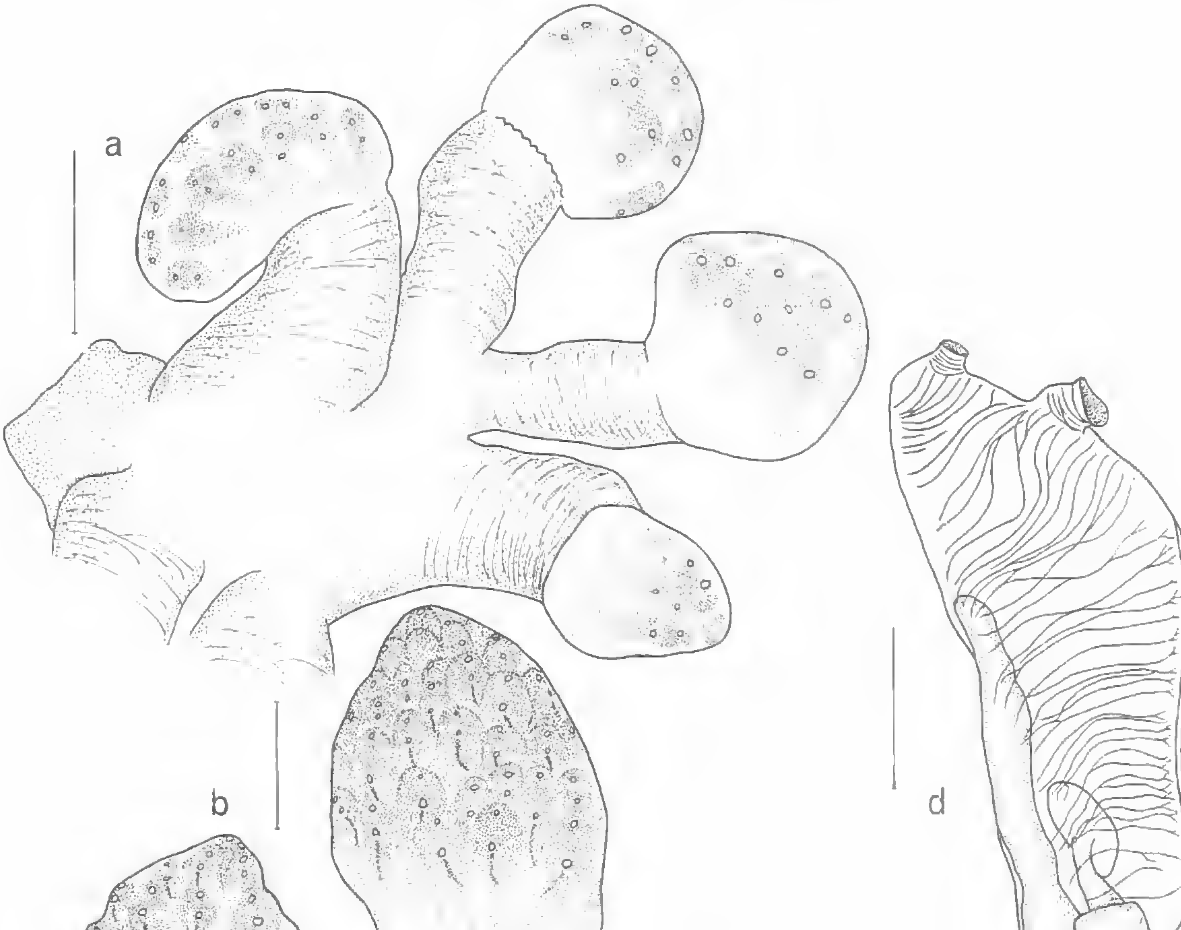


FIG. 21, *Nephtheis fascicularis*: **a**,**b**, colonies (QM GH2093 G12756); **c**, colony showing top of stalk with vascular reticulum (QM GH2093); **d**, zooid (QM G9258). Scales: **a**,**b**, 5mm; **c**, 2mm; **d**, 1mm.

large colonies with the stalk continuing up through the head to form a central axis are all from Roebuck Bay, Broome and there were no small colonies without the vascular network continuing up into the centre of the head recorded from that location. Van Name (1918) reported long colonies from the Philippines, up to nearly 20cm total length, that he likened to 'elongated pine cones' (Van Name 1918, p. 144). Although he does not mention the vascular network extending into the head it is probable that it does.

Colour also varies in some colonies. The western Australian ones are translucent (both living and in preservative). All other colonies in the newly recorded material are opaque blue, and this colour persists in the preserved specimens which have a conspicuous vascular network in the body wall that is not conspicuous in the colonies from Broome. However, Van Name observed similar colour variations in his Philippine material. It is likely that the variations in the extent to which the vascular network of the stalk penetrates the head, and in the intensity of pigmentation are, respectively, due to age and intraspecific variation, rather than genetic differences associated with an indigenous Roebuck Bay species isolated from populations in the Arafura Sea and to the north.

Roebuck Bay colonies found at the extreme low tide level, when exposed, continually drip water (*pers. comm.* N. Coleman).

Herdman (1899) believed these Roebuck Bay populations (see Saville Kent 1897) to be *Colella claviformis* Herdman, 1899 (< *Euclavella* n.gen. *claviformis*). Kott (1957a) suggested they could be *Sigillina cyanea*. However, in both cases similarities are only superficial and there are differences in the colonies as well as in the zooids. Both Herdman's and Kott's guesses were based on the similar general shape of the colony which consists of a strong, firm common stalk that raises the zooid-bearing head off the substrate. This colony type is found in other species of Holozoidae and also in the Polycitoridae and the Polyclinidae, and appears to be convergent.

The similarity of the colony and the zooids of this species to those of *Clavelina cylindrica* has been referred to above. The short zooid with short thoracic muscles and short gut loop that is found in *C. cylindrica* and *Nephtheis fascicularis* may be a convergent adaptation associated with the stalked rope-like colony with a layer of zooids surrounding a central axial stalk. However the presence of the prestomach and *Clavelina*-type larva suggests a phylogenetic relationship as well.

Family PYCNOCLAVELLIDAE new family

The family accommodates *Pycnoclavella* Garstang, 1891 and the new monotypic genus *Euclavella*, both containing species formerly in Clavelinidae.

The new family is characterised by its relatively small but thread-like zooids divided into thorax and abdomen, smooth apertures, no internal longitudinal branchial vessels, a long oesophageal neck, smooth stomach at the posterior end of the abdomen, and a posterior stomach in the pole of the gut loop rather than (as in Clavelinidae) in the descending limb. The anus opens at the base of the atrial cavity (unlike the Clavelinidae or Diazonidae where it opens some distance up the branchial sac). A vascular stolon contains a mesodermal septum. Gonads are reduced in size, the testis consisting of a compact group of follicles or (in one species) a single follicle. Only in *Euclavella* n. gen. do they spread out over the outside of the gut as they do in Clavelinidae. The ovary is always small, containing no more than about 6 eggs. Eggs are fertilised at the base of the oviduct and develop as they move anteriorly. The principal character separating the new family from Clavelinidae is the unique larva with 2 or 3 long, tubular adhesive organs invaginated into the anterior half of the larval trunk. They are placed one above the other in the anterior midline when 2 are present, but when 3 they retain the primitive triradial arrangement. Prior to settlement, or when pressure is applied to the trunk of the mature larva, these tubes evert, projecting out in the front of the larval trunk with the group of adhesive cells formerly at the base of the tube now on the tip of the everted organs. Larvae of many species of Pycnoclavellidae are also unusual in lacking an otolith in the cerebral vesicle. However, this is not universal throughout the family, and its absence may be a secondary adaptation, associated with the long sticky adhesive organs (Trason 1963).

Trason (1963) demonstrated similar tubular adhesive organs in larvae of *P. stanleyi* Berrill and Abbott, 1949 as those reported for larvae of other species known at that time, *viz. P. aurilucens* Garstang, 1891 from the English Channel (see Berrill 1947a) and *P. minuta* Millar, 1953b from Africa. Larvae are now known for all subsequently described species of *Pycnoclavella*, except *P. kottae* (Millar, 1960) and *P. aurantia* n.sp., and they all have these unique adhesive organs, as do the larvae of *Euclavella* n. gen. They appear unrelated to the stalked adhesive organs commonly found in *Clavelina* spp., which consist of a cone of columnar cells surrounded by a collar or cup of epidermal cells. The long, invaginated epidermal tubes of the Pycnoclavellidae could have evolved only from a simple, sessile, non-everting cionid-type adhesive organ.

Berrill (1947a) placed *Pycnoclavella* in Clavelinidae, assuming the vascular stolon with its terminal enlargement and mesodermal septum was an indication of a similar method of replication to that in *Clavelina* spp. However, Trason (1963) showed replication in *Pycnoclavella* was different from that in Clavelinidae. She maintained, with *Pycnoclavella* included, Clavelinidae was 'an artificial assemblage' (Trason 1963 p. 323). Trason (*loc. cit.*) demonstrated, in *Pycnoclavella stanleyi* Berrill and Abbott, 1949, that although the regenerating zooid remains connected to the stolonic vessel with its terminal expansion, it originates from horizontal division across the abdomen of the parent zooid; and the regenerative process involves epicardial tissue as in many other aplousobranch ascidians (but not in Clavelinidae).

Replication of *Euclavella* has not been investigated. The relationship between *Euclavella* and *Pycnoclavella* is, at this stage, based entirely on larval form.

Larvae of species of both Clavelinidae and Pycnoclavellidae are large, a characteristic of viviparous larvae of colonial species (see Annotated Glossary, above; and Kott 1985). Consequently, these families have a long evolutionary history as colonial organisms. However, at this stage, there is no indication of a relationship between the two forms of replication producing colonies in Clavelinidae and Pycnoclavellidae respectively; and therefore nothing to indicate if replication had evolved in a common cionid-like ancestor before either of these extant families separated from it. In fact, only the possession of smooth-rimmed apertures — a character that otherwise occurs only in some zooids of the Stolidobranchia simplified as a result of size reduction (e.g. in Polyzoinae) — suggests a common ancestor. Pycnoclavellid genera are distinguished from *Euherdmania* (Polyclinidae), which has similar larvae, and in which fertilisation is at the base of the oviduct, by the clavelinid-like characters of the zooids (smooth-rimmed apertures, smooth stomach walls and absence of a posterior abdomen).

In addition to the unusual larval adhesive organs and probably the process of replication, the large pigmented orange or green cells that so often predominate in both zooids and larvae are also characteristic of this family. In larvae these cells are usually present in the test, and they subsequently amass in the tip of the vascular process, and apparently colour adult zooids. Neither Berrill (1950) nor Trason (1963) believed they were the same as cells that Trason (1963 p. 311) observed 'moving in the circulatory system throughout the animal . . .' and that are 'seen in great numbers in the abdomen of the oozooid before budding occurs'.

Though records are few, possibly because colonies are cryptic and usually not intertidal, *Pycnoclavella*, found in Atlantic and Pacific oceans, and in tropical as well as temperate waters is especially well represented in Australian waters. *Euclavella* is known by only one species recorded from the coast of New South Wales and the North Island of New Zealand.

Genus **Pycnoclavella** Garstang, 1891

Type species: *Pycnoclavella aurilucens* Garstang, 1891

The genus contains colonial species with relatively small, partially embedded, or almost separate zooids, with a short thorax and long narrow abdomen. Eggs are fertilised in the base of the oviduct and continue their development as they pass up it to the atrial cavity. Larvae are characteristic of the new family, Pycnoclavellidae, having 3, or sometimes only 2, long, tubular, eversible adhesive organs. The otolith is often, but not always, absent from the larval cerebral vesicle (see *P. aurilucens*, *P. stanleyi*, as well as *P. minuta*, *P. detorta* and *P. elongata* n. sp.). However, a small otolith is present with the ocellus in *P. arenosa*, *P. diminuta* and *P. tabella* n.sp. Larvae of some *Pycnoclavella* spp. (*P. arenosa*, *P. stanleyi*, *P. aurilucens* and *P. minuta*) often (but not always) have the epidermis at the anterior end of the trunk thrown up into longitudinal ridges (referred to as ampullae) and furrows (that form pockets) around the adhesive organs.

Pycnoclavella is distinguished from *Euclavella* by smaller zooids, fertilisation of eggs in the base of the oviduct and partially separate zooids.

Probably *Archiascidia* is a synonym of *Pycnoclavella*. Deflection of the dorsal ends of the anterior and posterior rows of stigmata along the mid-dorsal line, described below for all *Pycnoclavella* except *P. elongata* n. sp., has been noted for *Archiascidia neapolitana* Julin, 1904 from the Mediterranean (see Brien 1948). Brien believed it a neotenous condition. However, the presence of dorsal languets associated with these deflections of stigmata suggest an evolutionary reduction in size of the branchial sac rather than a persisting embryological condition. It occurs in other small

TABLE 2. Summary of Characters of the Species of *Pycnoclavella* Recorded from Australia

Species	[1]Biogeographic description	[2]Range around Australia	Colony Organisation	Colour (living)	Thoraces (orientation to long axis of zooid)	Stigmata (number of rows)	Male follicles	Larval trunk (length, mm)	Adhesive organs; otolith
P. detorta	IWP,tr	Heron I.–Geographe Bay	zooids upright, separate; branching basal stalks	yellow-green translucent	90°	6	several, short	1.7	3; small
P. aurantia n.sp.	A,te	Nuyts Arch.	"	orange opaque	"	8	numerous, long	?	?
P. elongata n.sp.	A,te	Nuyts Arch.	"	"	in line	14	?	1.0	3; none
P. diminuta	WP,tr-te	Darwin–Lizard I.	"	white, yellow, blue, or brown; transparent or opaque	"	3	several, short	1.75	2; small
P. tabella n.sp.	A,te	Spencer Gulf–Portsea	"	white translucent, yellow stalk	"	3	one	0.8	2; small
P. arenosa n.sp.	A,te	Investigator and Bass Straits	abdomina embedded in axial common stalk; thoraces separate	yellow opaque	"	6	?	0.7	2; small

[1] A, indigenous; WP, western Pacific; IWP, Indo-West Pacific; tr, tropical; te, temperate. [2] Range given anticlockwise around the continent.

(reduced) zooids, *viz. Eudistoma* and *Cystodytes* (Polycitoridae) with 3 and 4 rows of stigmata, respectively. It probably is convergent rather than indicative of a phylogenetic relationship between Pycnoclavellidae and Polycitoridae.

The genus can be conveniently separated into 3 groups of species, based on colony form:

1. *Aurilucens* group contains *P. aurilucens* from the English Channel, *P. minuta* from tropical western Africa, and *P. arenosa*, with a common basal test mass in which the posterior ends of zooids are embedded. These species contain large pigmented morula cells in the larval test. *Pycnoclavella aurilucens* and *P. arenosa*, have, respectively, green and yellow larvae and adults. The colour of *P. minuta* is not known. Larvae have longitudinal ridges ('ampullae') at the anterior end of the trunk and adhesive organs are not as deeply invaginated as in other groups.
2. *Stanleyi* group contains *P. stanleyi* from California, *P. diminuta*, *P. tabella* n.sp. and *P. elongata* n.sp., with basal stolons but no common mass of test. These species also contain pigmented cells in the larval test, and both larvae and adults are orange in all except some specimens of *P. diminuta* — which have blue, white, or brown adult thoraces. Longitudinal furrows at the anterior end of the larval trunk have been detected only in *P. stanleyi*. Adhesive organs are always deeply invaginated.
3. *Detorta* group contains *P. detorta*, *P. kottae* from New Zealand, and *P. aurantia* n.sp. with thoraces turned through 90° Both *P. detorta* and *P. aurantia* have orange pigment, although the colour of *P. kottae* is not known. The larva is known only for *P. detorta*. It has 3 long adhesive organs and the oozooid is better developed than usual with the gut loop differentiated, longitudinal thoracic muscles and 6 rows of stigmata.

Pycnoclavella is diverse in Australian waters. Although zooids are small, colonies are striking when alive. Consequently they have been photographed frequently by SCUBA divers. *Pycnoclavella detorta* and *P. diminuta* are tropical species, while all others are temperate, possibly isolated from tropical ancestors, *e.g. Pycnoclavella aurantia* n.sp. is clearly related to *P. detorta*; and *P. tabella* n.sp. to *P. diminuta* and both pairs probably are sister species.

KEY TO THE SPECIES OF *PYCNOCLAVELLA* RECORDED FROM AUSTRALIA

1. Thoraces turned through 90°, the atrial aperture terminal 2
   Thoraces not turned through 90°, the branchial aperture terminal 3
2. Stigmata in 6 rows .... *P. detorta*
   Stigmata in 8 rows .... *P. aurantia* n.sp.
3. Stigmata in 3 rows 4
   Stigmata in > 3 rows 5
4. Zooids thread-like, with less than 20 stigmata per row.................. *P. tabella* n.sp.
   Zooids not thread-like, with more than 20 stigmata per row .... *P. diminuta*
5. Abdomina embedded in a branching axial stalk; stigmata in 6 rows .... *P. arenosa*
   Abdomina not embedded in a branching axial stalk; stigmata in > 6 rows .... *P. elongata* n.sp.

The only confirmed species known from the western Pacific and not yet recorded from Australia is *Pycnoclavella kottae* Millar, 1960, from the North I., New Zealand, distinguished from *P. detorta* and *P. aurantia* n.sp. by its more numerous (13 to 27) rows of stigmata.

Pycnoclavella arenosa (Kott, 1972)
(Fig. 22. Plate 5d)

Oxycorynia arenosa Kott, 1972b, p. 167.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, QM GH4226 GH4360).

PREVIOUSLY RECORDED South Australia (Investigator Strait — MV H168 holotype, MV H169 paratype Kott 1972b).

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are arranged around cylindrical and irregularly branching central common stalks 1.0 to 1.75cm in diameter and up to 9cm long. The outer layer of test, through which pass the oesophageal necks of the zooids, is sandy. Separate thoraces of the zooids project out beyond the sand along the length of the branching common stalks. The thoracic test is free of sand and transparent. The central test of the stalk, inside the sand, is soft, transparent, and contains abdomina of zooids and their long vascular stolons. In preservative morula blood cells in the zooids (especially crowded in the branchial sac) are dark and can be seen through the outer coat of sand. The layer of test around zooids contains circular brown plates resembling the spherical bodies in the test of *Pycnoclavella diminuta*, but more crowded.

Colour photographs of the newly recorded specimen from Erith I., Bass Strait, show the thoraces as yellow, but in preservative they are purple-brown.

INTERNAL STRUCTURE: The zooids are less than 1cm long, the abdomen up to 4 times the length of the thorax. Apertures are smooth-rimmed. Twelve broad longitudinal muscle bands, with the formula 3E,6B,3D on the thorax extend onto the abdomen.

There are 6 rows of 20 rectangular stigmata and the dorsal ends of the anterior and posterior rows turn anteriorly and posteriorly, respectively, to extend along each side of the mid-dorsal line. The smooth, almost spherical stomach is in the posterior end of the abdomen and an oval posterior stomach is in the pole of the gut loop. In all examined specimens the body wall around the posterior end of the gut loop, and the space enclosed by it, are crowded with the trophozooite cells characteristic of a vegetative condition.

Up to 8 embryos line up in the oviduct in zooids from the newly recorded colony from Bass Strait, which was collected in May. Larvae are relatively small (trunk 0.7mm long). The tail is wound three-quarters of the way around the trunk. Just before larval release it is curved up across the left side of the anterior end of the trunk. Internal structure is difficult to discern because of the dark blood corpuscles in the larval test and haemocoelic cavity. There is a large ocellus and a small otolith. Two inverted, tubular adhesive organs at the anterior end of the trunk are not as large as in other species of the genus. At the anterior end the trunk epidermis folds to form 8 long furrows making ridges around the adhesive organs (referred to as ampullae by Berrill and Abbott 1949, and Trason 1963). The furrows are filled with the dark morula cells. There are 2 rows of large stigmata.

REMARKS: Colonies of this species are reminiscent of *Clavelina cylindrica*, with zooids projecting out from cylindrical axial stalks. However, in *C. cylindrica* the whole zooid projects while in *P. arenosa* it is only the thoraces that do. Further, both larvae and zooids of this species share certain characters with other *Pycnoclavella* that distinguish them from *Clavelina*. They are smaller, have relatively longer abdomina, fewer and shorter rows of stigmata with the anterior and posterior rows deflected along the mid-dorsal line, the stomach at the posterior end of abdomen, and the posterior stomach in the pole of the gut loop. Larvae are unusual, possessing an otolith and shorter adhesive organs than usual. The species is distinguished from others recorded from Australian waters by its colony form and blood cells that appear dark in preservative.

Pycnoclavella aurilucens, Garstang, 1891 (? < *Clavelina nana* Lahille, 1890; see Berrill 1950) from the English Channel and *P. minuta* Millar, 1953b from Africa have colonies similar to those of the present species, with the posterior ends of the zooids embedded in common basal test and at least the thorax protruding from it, rather than

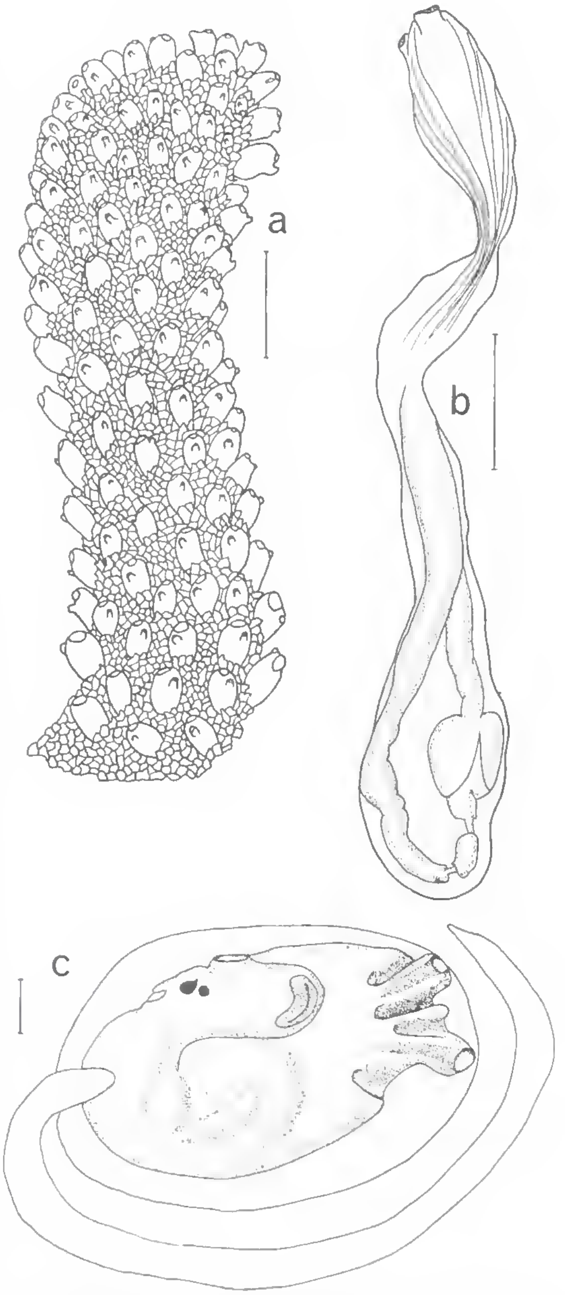


FIG. 22. *Pycnoclavella arenosa*: **a**, colony (holotype, MV H168); **b**, zooid (paratype MV H169); **c**, larva (QM GH 4226). Scales: **a**, 5mm; **b**, 1mm; **c**, 0.1mm.

being joined by basal connecting stalks as in *P. diminuta* and related species. However, this basal test is olive green and the tadpole larvae contain green pigment, sometimes being uniform green (*Clavelina nana*). In the larval test and adult zooids of *P. arenosa* the morula cells that are purplish brown in preservative are probably yellow in life. They may be homologues of orange cells described by Trason (1963) in the larval test of *P. stanleyi* where they have the same distribution as in *P. arenosa*. In *P. arenosa* the cells in the adult circulatory system presumably confer the colour on the zooids in the same way as its orange cells affect the adult zooids of *P. stanleyi* (see Trason 1963).

Pycnoclavella aurantia n.sp.

(Fig. 23a. Plate 5e)

DISTRIBUTION

TYPE LOCALITY: South Australia (Franklin I., Nuyts Archipelago, 15m, breaking reef, coll. N. Holmes, location C, February 1983, holotype QM GH2295).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of clumps of balloon-like heads supported on long, thin, straight stalks arising from a mass of common basal test up to 5mm thick. The balloon-like head is the thorax of the zooid, and the stalk is the oesophageal neck, the lower half to one-third of the abdomen being embedded in the basal test. The free part of the zooids is up to 1cm long, of which the head is from one-quarter to one-third. In life the expanded head is wider than longer. However, the thorax is turned through 90° on the top of the stalk (as in *Pycnoclavella detorta*) so that the branchial siphon is on one side and the atrial aperture is terminal. Thus the width of the head is actually the length of the thorax. Living specimens have uniformly orange stalks and heads.

INTERNAL STRUCTURE: The body wall is delicate and transparent. The ventral border of the zooid curves down toward the top of the stalk, and continues around the posterior end of the pharynx to the oesophageal opening in the position usually occupied by the retropharyngeal groove. Longitudinal and oblique muscle bands have the formula: 5E,3B,3D. Oblique muscle bands run from the anterior half of the endostyle. In some contracted thoraces oblique muscles are reduced to 3. Longitudinal muscles and the most anterior of the oblique ones extend onto the dorsal surface of the abdomen and continue along it in a broad band. Four more posterior, oblique muscle bands, having crossed the posterior end of the pharynx with the oesophageal end of the endostyle running along it, form a band extending along the ventral surface of the abdomen.

About 16 long, curved branchial tentacles, with about the same number of smaller tentacles encircle the base of the branchial siphon. However, these were difficult to count, and rudimentary tentacles were not detected. The neural gland opening is a simple, circular aperture projecting into the pharynx.

There are 8 rows of about 50 stigmata. However, the anterior and posterior rows of stigmata are longer and extend along the mid-line where they add to the area of the branchial sac, forcing it out to form dorsal pockets or pouches on each side of the dorsal lamina. Bands of unperforated pharynx are both anterior and posterior to the perforated area. The oesophagus is long, extending along the right side of the rectum down to the stomach in the posterior end of the abdomen. Gonads are in the gut loop posterior to the stomach. They consist of a small group of up to 5 ova in the middle of a mass of relatively long, pyriform follicles. The testis follicles are mature in the holotype, but the ova are not. Larvae of this species are not known.

REMARKS: The species differs from *Pycnoclavella detorta* in its having more rows of stigmata, slightly fewer muscle bands, and uniformly orange living colonies (instead of the iridescent green and gold of the tropical species). It is probable that *P.aurantia* is a sister species of the more widely distributed tropical *P.detorta*.

Pycnoclavella detorta (Sluiter, 1904)

(Fig. 23b-e. Plate 5f)

Podoclavella detorta Sluiter, 1904, p. 6. Kott, 1957b, p. 130.

Clavelina detorta: Van Name, 1918, p. 133. Millar, 1975, p. 209. Monniot 1988, p. 202.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 792.83; Geographe Bay, 13.84). Queensland (Heron I., QM GH4079; Wistari Reef, QM G9488 G11897. Philippines (QM GH527 GH529 GH532).

PREVIOUSLY RECORDED: New Caledonia (Monniot 1988). Indonesia (Sluiter 1904). Philippines (Van Name 1918; Millar 1975). Red Sea (Kott 1957b).

The species appears to have a wide range in the tropical western Pacific from the Philippines and south to the Capricorn Group in the Great Barrier Reef, and on the western Australian coast even further south to Geographe Bay. It has been taken down to 40m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of large clumps of separate zooids up to 3cm long arising from common basal test. The test over

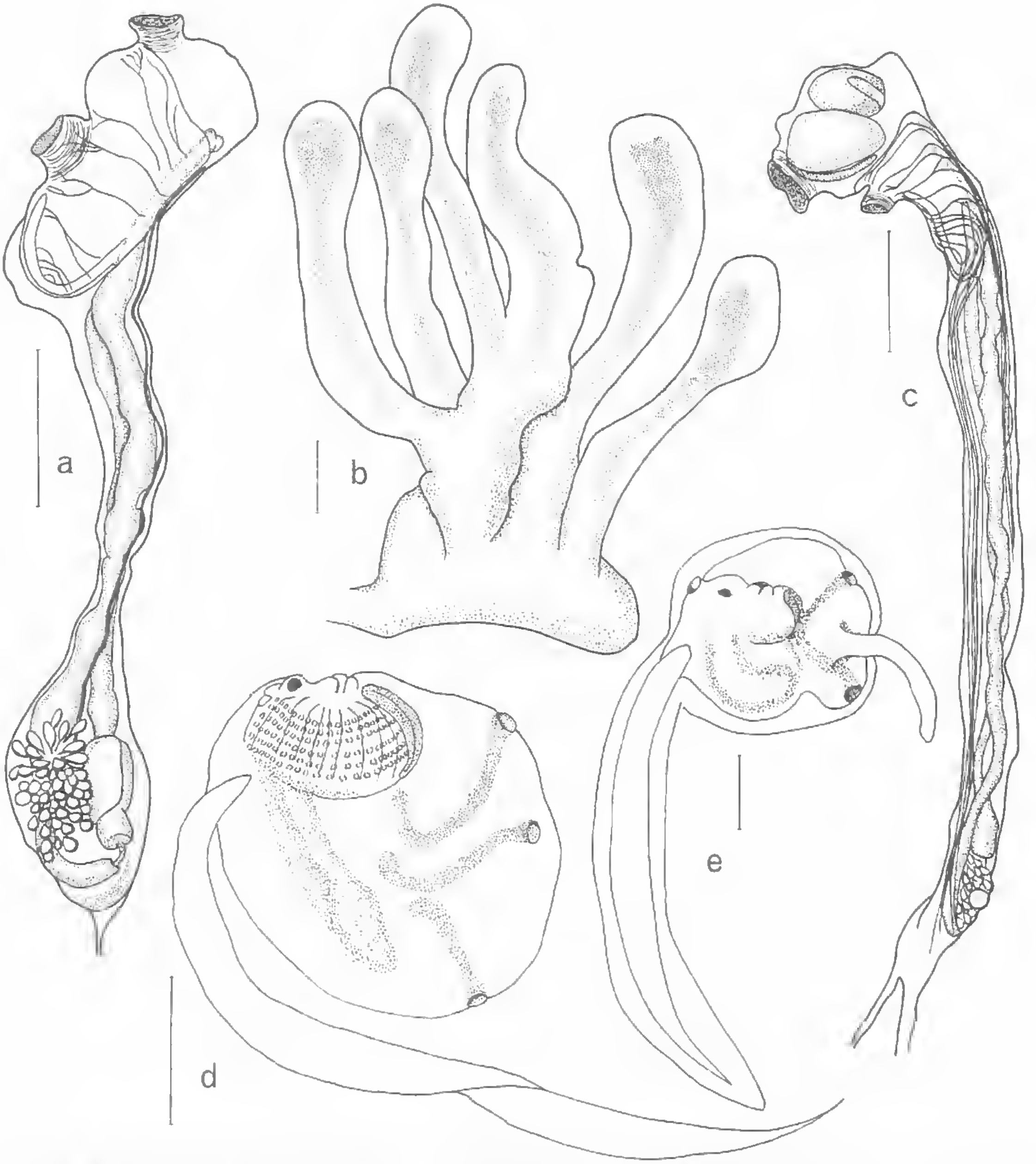


FIG. 23, *Pycnoclavella aurantia* n.sp.: **a**, zooid (holotype QM GH2295). *Pycnoclavella detorta*; **b**, colony (QM G11897); **c**, zooid (QM G11897); **d,e**, larvae, one with a tubular adhesive organ everted (QM G9488). Scales: **a–c**, 2mm; **d,e**, 0.5mm.

thoracic parts of zooids is delicate and in life this is inflated and balloon-like. The test becomes firmer over the long narrow abdominal stalk. The branchial sac is bent over through 90° so the atrial cavity and aperture are terminal, the branchial aperture on one side, and the lower end of the endostyle and the retropharyngeal groove with the oesophagus and the rectum running alongside are on the other side of the stalked head. The terminal free end of the zooid has the dorsal lamina across it and the oesophagus opening at its dorsal edge.

In preservative zooids are colourless, but in life have greenish irridescent patches around the branchial aperture and over the dorsal ganglion, a wide patch of orange across the dorsal surface behind the base of the branchial siphon, and intense orange in the endostyle and in the whole of the abdomen.

INTERNAL STRUCTURE. The unusual orientation of the thorax is readily observed in living zooids owing to the bright orange of endostyle and rectum. The thorax occupies only about one-eighth of the total length of the zooid, the greater part being the long oesophageal neck. The stomach is at the posterior end of the body. The zooid extends almost to the basal stolon, one or two short vascular stolons lie at the posterior end of the abdomen.

The body wall is delicate. Conspicuous muscle bands, with the formula 8E.4B.3D, extend from the branchial siphon, the intersiphonal mid-line, and the anterior half of the endostyle to the other side of the thorax (posteriorly positioned in these zooids). Muscle bands from the intersiphonal space and the branchial siphon (longitudinal muscles) cross the posterior end of the pharynx where the endostyle continues to the oesophagus in the position usually occupied by the retropharyngeal groove. Muscles then turn down to run along the dorsal side of the abdomen in a band with some of the oblique muscles from the anterior end of the endostyle. The more posterior oblique muscles cross the posterior half of the endostyle (the endostyle curving down into the stalk in a deep arc or V) and then extend into a broad band running down the ventral side of the abdomen. Fine circular bands encircle each aperture. Branchial tentacles are slender, in 3 circles, the most posterior one with the 6 longest alternating with 6 of moderate length, and about twice the number of rudimentary tentacles in the anterior circle. The neural gland opening is a simple transverse oval or kidney-shape.

There are 6 rows of stigmata with about 24 in a middle row. Although the endostyle is bent down in a deep arc and the dorsal lamina is straight across the anterior end of the zooid, the anterior and posterior rows of stigmata are not shorter than the middle rows, the shorter distance between each end of the endostyle and the dorsal lamina being compensated for by the deflection of the dorsal stigmata along the mid-line dorsal to the areas of unperforated pharynx anterior and posterior to the perforated area. This creates pouches that project up on each side of the dorsal lamina at the dorsal ends of the anterior and posterior rows of stigmata. The oesophagus is long and narrow, extending down to a shield-shaped stomach near the posterior end of the abdomen. The stomach has a suture line but no structural ridges or folds. Gonads, consisting of rather large pyriform male follicles and a group of 5 or 6 small ova, lie in the gut loop behind the stomach.

Embryos complete their development in the atrial cavity at the top of the free end of the zooid, where up to 4 large tailed embryos can be found at a time, all at different stages of development. Embryos are present in colonies from Wistari Reef in August.

Larvae are large, the trunk 1.7mm with a broad tail that encircles about three-quarters of the circumference of the trunk. The anterior half of the trunk is penetrated by 3 long tubular invaginations of larval epidermis with the group of adhesive cells in the base of the tube. When these adhesive organs evert the front of the trunk becomes flattened. Before release of larvae these organs will evert if slight pressure is applied to the trunk, even in the preserved material. An ocellus but no otolith occurs in the cerebral vesicle. The larval test lacks the darkly pigmented morula cells found in *P. diminuta*, *P. tabella* n.sp and *P. arenosa*. There are five rows of short stigmata in the branchial sac.

REMARKS. *Pycnoclavella aurantia* n.sp. from South Australia and *P. kottae* Millar from the North Island, New Zealand, appear close relatives of this tropical species. Both have separate zooids with the branchial sac turned through an angle of 90°, however both have more rows of stigmata — *P. aurantia* has 8 and *P. kottae* has from 13 to 27.

Although developing embryos have not been observed in the oviduct of the newly recorded material, Van Name (1918 p. 134) reported them to be present in the 'proximal part of the abdomen' as well as in the atrial cavity. Certainly in the present collection embryos in the atrial cavity are all tailed larvae, which have already have undergone a period of development. It is most likely that this began at the base of the oviduct.

The horn-like projections of the test reported by Millar (1975) were not observed in any of the present specimens, not even those recorded from the Philippines.

Pycnoclavella diminuta (Kott, 1957)

(Fig. 24, Plate 6a–f)

Clavelina diminuta Kott, 1957a, p. 89.

Pycnoclavella diminuta: Millar, 1963a, p. 715. Kott, 1972b, p. 170 (part, not small specimen from Tipara Reef = *Pycnoclavella tabella* n.sp.)

Clavelina nodula Kott, 1972b, p. 166.

Archidistoma richeri Monniot, 1988, p. 199.

Archidistoma rubripunctum Monniot, 1988, p. 200.

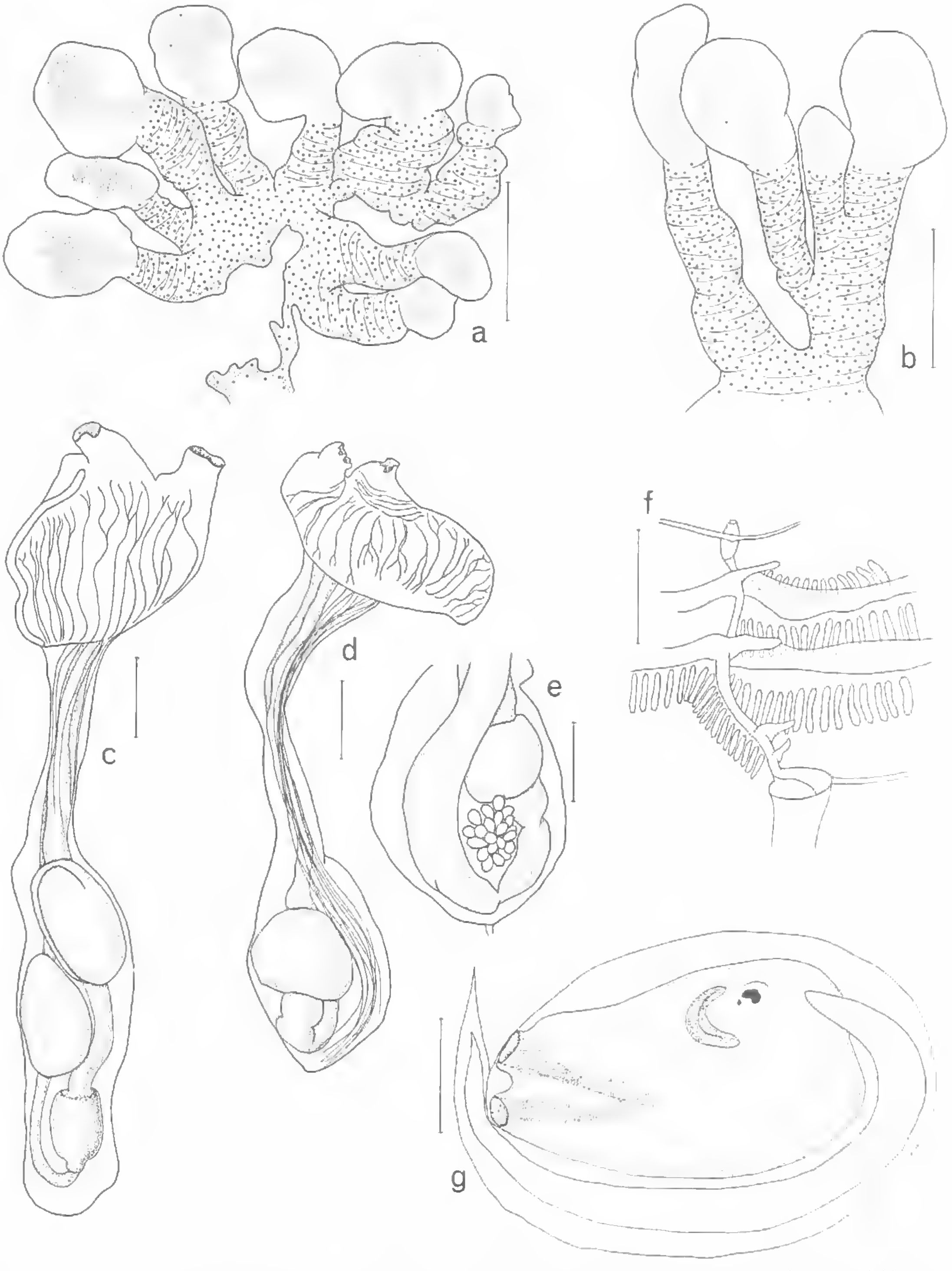


FIG. 24, *Pycnoclavella diminuta*: **a,b**, colonies (QM GH1194 GH1302); **c,d**, zooids (QM GH4083 G10162); **e**, abdomen showing testis (QM G10162); **f**, portion of branchial sac showing posterior row of stigmata extending posteriorly alongside mid-dorsal line (QM GH324); **g**, larva (QM GH4083). Scales: **a,b**, 5mm; **c–e**, 1mm; **f,g**, 0.5mm.

Distribution

New Records: Western Australia (Exmouth Gulf, QM GH4083 GH4084; Shark Bay, WAM746.83 982.83; Houtman's Abrolhos, WAM 372.80; Rottnest I., QM GH4089). South Australia (Great Australian Bight, GH1283 GH1302 GH2293 GH2389). New South Wales (Lord Howe I., QM GH53 GH4373 GH4377). Queensland (Heron I., QM GH4081 GH4089; Lizard I., QM G10162 G11994 GH324 GH3117). Northern Territory (Darwin, QM GH4293). Philippines (QM GH457–8 GH492 GH534 GH545–8 GH4109 GH4112–3 GH4118).

Previously Recorded: Western Australia (Cape Boileau — Millar 1963a; Rottnest I. — AM Y1193–5 Kott 1957a). South Australia (Great Australian Bight, Spencer Gulf, St Vincent Gulf — SAM E2038 Kott 1972b). New Caledonia (F. Monniot 1988).

The species is known from 5 to 20m, usually in caves and under ledges. It is apparently a tropical western Pacific form extending around the Australian coast. The collection of only a single small colony from Heron I. is surprising in view of the intensity of collecting that has taken place at that location.

Description

External Appearance: Living colonies consist of a mass of spherical heads, about 5mm in diameter, on narrow straight stalks up to 2cm long that arise from a basal common mass of test. The test on the stalks is gelatinous but rather firm and almost opaque, while that on the head is glassy, soft and usually mutilated in the preserved specimens. In preservative the stalks are wrinkled and thicker than in life with brown oily-looking vesicles scattered through the test. These vesicles, of various sizes, the largest in the internal test against the body wall of the zooid, have not been seen in the living colonies, which are variously referred to as 'light globe', 'blue-pod', 'yellow-pod', 'brown-pod' and 'white-bead' ascidians, indicating a wide colour diversity. This is not associated with the geographic location of the populations sampled and does not reflect morphological differences. In the Philippines, collector's notes refer to colonies as white, orange, purple and blackish with white markings. There are both brown and blue colonies from Exmouth Gulf; South Australian colonies have white heads with yellow stalks or are uniformly yellow; and the Lizard I. specimens are deep blue. The colour of the single small colony collected from Heron I. is not known. The pink colour noted in a small colony from Darwin (QM GH4293) may have been caused by the masses of nauplius larvae of a parasitic copepod.

The head contains the thorax of the zooid, in life expanded into the characteristic spherical shape. The long, narrow abdomen occupies the stalk and usually extends into the basal test mass.

Internal Structure: The body wall is delicate, with distinct muscle bands with formulae 5E,3B,3D (both blue and brown colonies from Exmouth Gulf); 7E,7B,3D (Lizard I.); 4E,4B,4D (Heron I.); 9E,11B,6D (Great Australian Bight). The number of muscle bands increases with size and robustness of zooids — specimens from South Australia being more robust than most others. Muscles extend along the abdomen to its posterior end. Branchial tentacles are in concentric circles, 6 larger tentacles posteriorly alternating with 2 smaller tentacles. Rudimentary tentacles were not observed, although there is a circle of flat projections of the body wall in the position where they are usually found. The neural gland opening is a simple, circular aperture projecting slightly into the lumen of the pharynx. A tongue-like flap projects posteriorly along the mid-line behind the prepharyngeal groove.

There are 3 rows of 40 to 60 stigmata — the count being done in the middle row — and an expanse of unperforated pharyngeal wall both anterior and posterior to the perforated region. The posterior row of stigmata on each side continues posteriorly along the dorsal lamina into the unperforated part of the pharynx, and the branchial sac projects out on each side of the dorsal lamina in this region. About 20 extra stigmata are added to the posterior row in this way. Four dorsal languets lie across the dorsal sinus — one each between the first and second, and the second and third rows of stigmata, and 2 close together on the posterior part of the dorsal sinus where the extra stigmata are located. The oesophagus is long, extending, alongside the rectum, to the posterior end of the abdomen where the smooth-walled, almost spherical stomach occurs. Internally the stomach sometimes, but not always, has some fine longitudinal ridges. A short, relatively narrow intestine curves around in the posterior end of the abomen and opens into the rectum. There is a bilabiate anus at the posterior end of the atrial cavity. Gonads consist of a small bunch of pyriform testis follicles in the posterior end of the gut loop. Two or 3 embryos are found in the oviduct, although no more than a single egg has been found in association with the testis follicles in the loop of the gut. Eggs are fertilised at the base of the oviduct and continue their development as they pass up it, being found at progressively later stages of development.

Embryos were found in Lizard I. colonies collected in November (QM GH10162), but not in January, April or July; there were no larvae in Shark Bay colonies in April; South Australian colonies had no larvae in March or April in 2 successive years. Apparently the breeding season is restricted to late spring and zooids do not produce many eggs — the ones they do produce are large. The larval trunk is 1.75mm long. The tail, which is particularly broad, just reaches the anterior end of the trunk and its tip curves around in the mid-line over the apertures of the 2 invaginated tubes of the adhesive organs. There is an ocellus and a minute otolith. Crowded, darkly pigmented morula cells lie in the larval test of both trunk and tail, and, at the anterior ends of the trunk, circular groups of cells appear identical with the vesicles in the adult test. There are 2 rows of stigmata.

REMARKS: The species is conspicuous owing to its brilliant colours. It is surprising that it has not previously been recorded from the tropical western Pacific — possibly its spherical thoraces have been mistaken for mollusc eggs. It is characterised by its 3 wide rows of stigmata, the recurved posterior row (which also occurs in *P. detorta* and *P. aurantia*), the oily-looking vesicles in the test of the stalk, and the large larva. An otolith is unusual in *Pycnoclavella*. One occurs in *P. tabella* n.sp., a closely related species which has similar inclusions in the test of the stalk. However a small otolith as well as the ocellus occurs also in *P. arenosa* n.sp. which is in a different species group from the present species. This suggests that the loss of the otolith is an intrageneric convergent adaptation that occurs in parallel within the genus.

Specimens assigned to new species in the genus *Archidistoma* by Monniot (1988), have all the characteristics of *Pycnoclavella*, including the larvae, *viz.* small otolith, 2 adhesive organs, long larval trunk, and position of the anus at the posterior end of the atrial cavity. They appear synonyms of the present species.

Pycnoclavella elongata n.sp.
(Fig. 25. Plate 6g)

DISTRIBUTION

TYPE LOCALITY: South Australia (Franklin I., Nuyts Archipelago, just offshore N of West I., 8-10m, rock outcrops and some sand patches, coll. W. Zeidler, P. Aerfeldt *et al.*, 22.2.83, holotype SAM E1980; Franklin I., Nuyts Archipelago, on rock amongst breaking reef, 15m coll. N. Holmes, paratypes QM GH4082, SAM E1981).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of clumps of elongate heads each on a narrow straight stalk joined by basal stolons that tangle and adhere to one another. Heads are about 1cm long and 4 to 5mm at their widest (halfway along) and they narrow toward the stalk at their anterior ends. Stalks of preserved colonies are about 8mm long, but are wrinkled and probably are larger in life. The test over the head is soft and flexible, but firmer on the stalk. Both head and stalk of living colonies are uniformly opaque orange. Sometimes the lower half of the stalk and the basal test are invested with sand. Apertures are close together, on opposite sides of the narrow free end of the zooid, and are turned away from one another.

INTERNAL STRUCTURE: Zooids are between one and 2cm long, of which the thorax is one-quarter to one-third of the total length. The thoracic muscles are strong with formula 10E,3B,4A. They extend down along the abdomen. Six long, branchial tentacles alternate with 2 moderately sized ones in an anterior circle. A circle of minute flat projections of the body wall anterior to these 2 circles of tentacles may be rudimentary tentacles. The simple, circular neural gland opening projects slightly into the pharynx.

There are 14 rows of stigmata with about 30 stigmata per row. The last row of stigmata is not curved posteriorly along the dorsal lamina as it is for many other species of this genus with a more reduced thorax. The oesophagus is long, extending to the smooth, round stomach at the posterior end of the abdomen. Male follicles were not detected. They may have matured before the ova.

Up to 10 large embryos in a developmental sequence are present in a single line up the oviduct, toward the thorax. The larval trunk is about 1mm long. Larvae have the usual 3 long, tubular adhesive organs, triradially arranged, projecting back into the trunk from the anterior end. An ocellus, but no otolith, is in the cerebral vesicle. A few dark morula cells occur in the larval test of the trunk, and none in the test of the tail.

REMARKS: The branchial sac is particularly long and narrow for this genus, and the species can be distinguished by its unusually numerous rows of stigmata, with anterior and posterior rows not extended along the dorsal mid-line. The colour of the living zooids resembles that of *Pycnoclavella aurantia* n.sp., which, as well as having a different body shape and number of rows of stigmata, has differently oriented thoraces — the present species having both apertures terminal while in *P. aurantia* they are at right angles to one another, the branchial aperture on one side and the atrial terminal.

The species is possibly most closely related to *P. diminuta* and *P. tabella* n.sp., having a similar colony, but is distinguished from them by its longer thorax, the lack of vesicles in the test, and the crowded morula cells in the larval test.

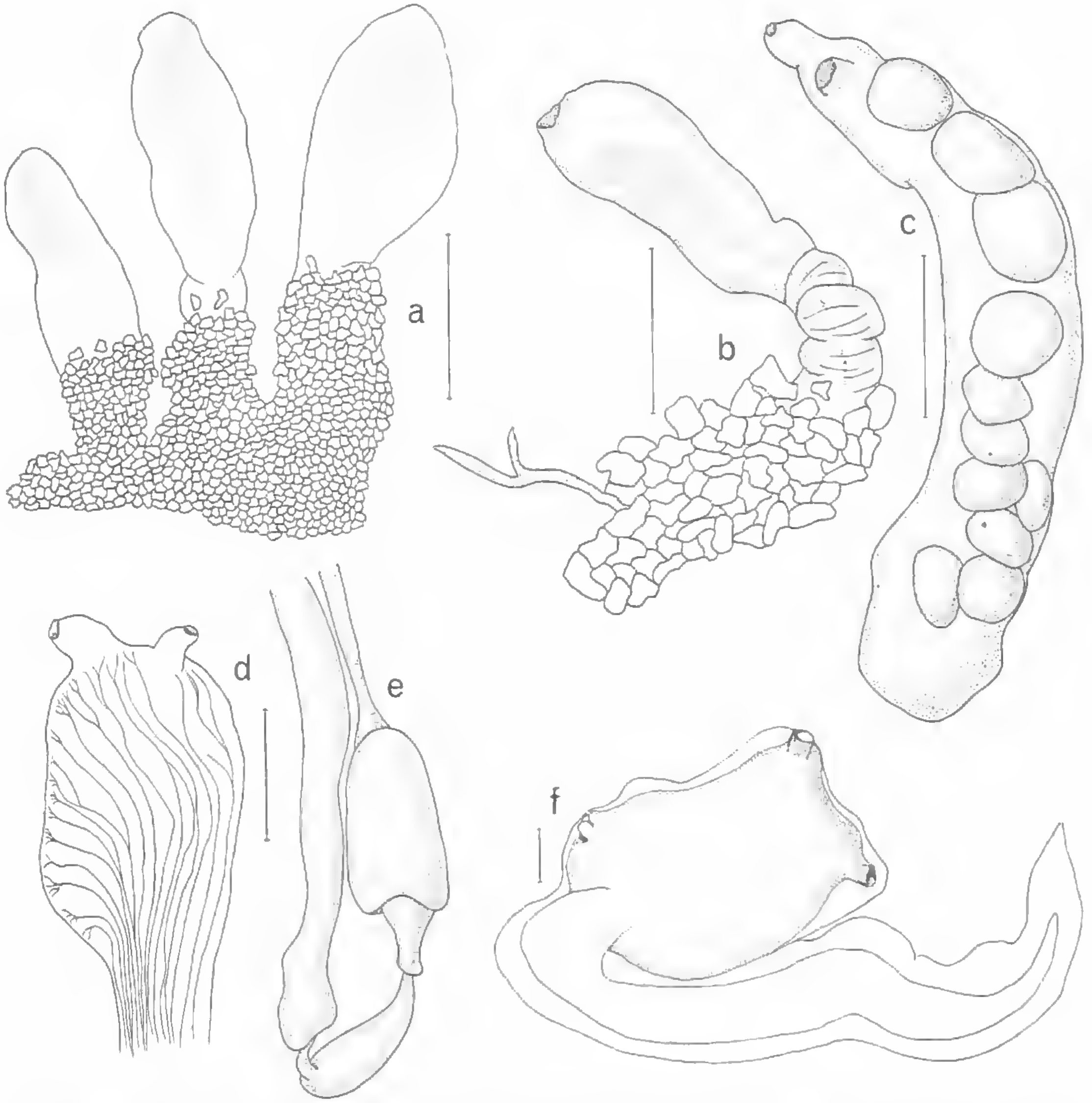


FIG. 25, *Pycnoclavella elongata* n.sp.: **a**, colony (holotype SAM E1980); **b**, single zooid isolated from colony (paratype SAM E1981); **c**, zooid removed from test showing incubating embryos (holotype SAM E1980); **d**, thorax showing muscles (holotype SAM E1980); **e**, gut loop (holotype SAM E1980); **f**, larva (holotype SAM E1980). Scales: **a,b**, 5mm; **c**, 2.5mm; **d,e**, 1mm; **f**, 0.2mm.

Pycnoclavella tabella n.sp.

(Fig. 26, Plate 6h)

Pycnoclavella diminuta: Kott 1972b, p.170 (part, small specimens from Tipara Reef).

DISTRIBUTION

TYPE LOCALITY: Victoria (Portsea, on reef, 1.8m, coll. N. Coleman, 4.6.77 holotype QM G10161). South Australia (Tipara Reef, Spencer Gulf, 11m, coll. Shepherd, 24.9.71, paratypes QM G9257, SAM E1982).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of masses of thin, upright sandy stalks (1.5cm high) from which the soft sand-free thoracic parts of the zooids protrude. The sandy stalks, all the same height, have fine hair-like extensions of the test to which sand adheres, and by which they adhere to one another to form a sandy mass that, in life, is covered with the crowded white spherical bead-

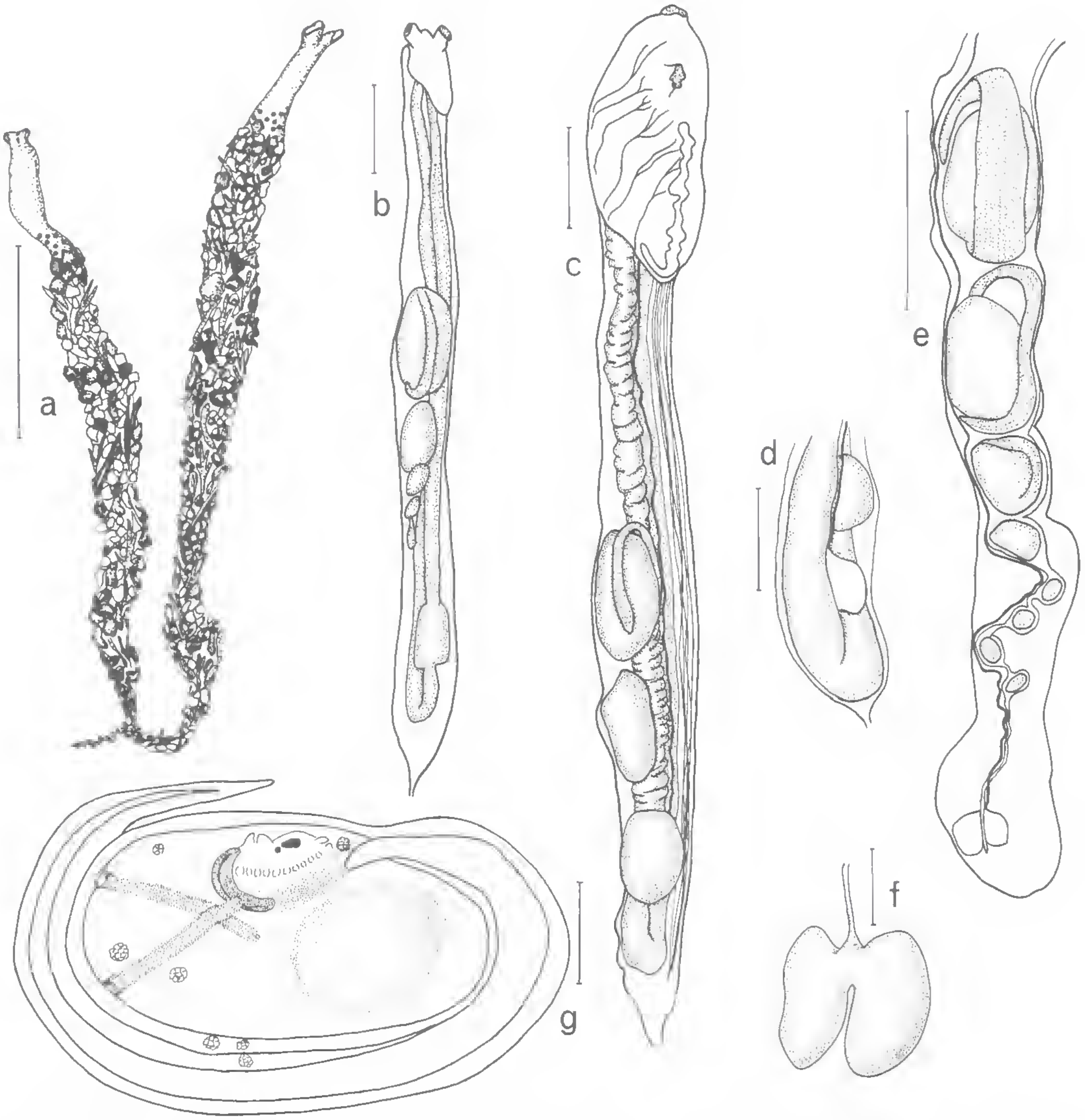


FIG. 26, *Pycnoclavella tabella*, n.sp. (QM G10161): **a**, colony; **b,c**, zooids; **d**, posterior end of gut loop showing testis between descending and ascending limbs; **e**, abdomen with gut loop removed showing testis, ovary and incubating embryos in oviduct; **f**, testis divided into 2 lobes; **g**, larva. Scales: **a**, 5mm; **b,c,e**, 1mm; **d**, 0.5mm; **f**, 0.1mm; **g**, 0.2mm.

like expanded thoraces. Basally, the sandy stalks taper into fine stolons which connect zooids to one another and have side branches that fix them in the substrate. Beneath the adherent sand the test of the stalk is slightly firmer than that of the thorax, and has brown vesicles scattered through it as in *P. diminuta*.

INTERNAL STRUCTURE: The zooids themselves are thread-like, up to 1cm long, with long vascular stolons that extend into the base of the stalk. The thorax is only about one-tenth of the length of the abdomen. The body wall is delicate with conspicuous longitudinal and oblique muscle bands with formula 3E,3B,2D. Muscles continue along the length of the abdomen. Apertures are close together on the free anterior end of the thorax.

There are 3 rows of up to 20 stigmata in the small, narrow thorax. An expanse of unperforated pharynx exists anterior and posterior to the stigmata, with the first and third rows turned, respectively, anteriorly and posteriorly along the dorsal mid-line. The long oesophagus opens into the small, spherical stomach in the posterior end of the abdomen. The testis is in the loop of the gut posterior to the stomach. It is a single, flat, sometimes bilobed, follicle narrowing anteriorly to the vas deferens. It is visible on the left side of the gut loop. In both specimen lots examined a series of up to 7 developing embryos occur in the oviduct, progressively better developed as they pass up the oesophageal neck to the thorax. Eggs are produced one at a time. Fertilisation apparently occurs just anterior to the stomach, where short intervals of duct between the proximal 4 eggs stain blue in haematoxylin indicating that sperm are present. In view of the narrow diameter of the oviduct which the large, developing embryos completely fill, sperm must be present toward the base of the oviduct before ovulation begins, and must persist there to fertilize the eggs as they are produced. Oviduct and vas deferens are closely associated for the whole of their length.

Larvae are relatively large, with a trunk 0.8mm long and with the broad tail wound almost all the way around the trunk. They have 2 inverted tubular adhesive organs at the anterior end of the trunk, in the median line. There is a large ocellus and a minute otolith. The larval test has brownish pigment spots that probably develop into the spherical bodies found in the adult test. The species appear more prolific than most others in the genus. Embryos are present in both June and September, and are more numerous than in other species.

Remarks: The species is related to *Pycnoclavella diminuta*, both species having only 2 adhesive organs in the larva, a larval otolith, a terminal branchial aperture, and the same brown vesicles in the test of the stalk. However, the present species is much smaller and less robust than *P. diminuta*, has fewer stigmata per row, fewer muscle bands, a sandy coat on the stalks, and a single, lobed testis follicle. The otolith, like that of *P. diminuta*, is minute and was overlooked by Kott (1972b), as was the fact that there were only 2, rather than 3 adhesive organs. The same anterior and posterior extensions of the first and third rows of stigmata along the dorsal mid-line are present as in most species of the genus.

Dumus areniferus, a species of the Euherdmaniinae, has similar colonies formed by the close adherence of small, upright, thread-like zooids, each in its own covering of sand-invested test.

Genus **Euclavella** n.gen.

Type species: *Colella claviformis* Herdman, 1899.

The genus contains a single species. It has a fleshy, stalked colony with completely embedded *Clavelina*-like zooids regularly arranged and opening to the surface all around the rounded to oval head. Vascular stolons with a mesodermal septum project down into the thick, fleshy stalk. The branchial tentacles are in 3 concentric circles as in *Clavelina*. Larvae have the tubular, invaginated adhesive organs of the family Pycnoclavellidae. There is a well developed ocellus in the cerebral vesicle, but no otolith. There are similar larvae with tubular adhesive organs and no otolith in *Pycnoclavella* spp. and the Euherdmaniinae. The closest phylogenetic relationship for the genus appears to be with *Pycnoclavella*, from which it is separated by its embedded zooids and the presence of a brood pouch in which fertilisation takes place. It is also distinguished from *Pycnoclavella* by the firm, opaque test in which the zooids are embedded, instead of the layer of soft transparent test that covers the thoraces of the zooids of *Nephtheis* and *Clavelina* as well as *Pycnoclavella*. The test of the whole zooid bearing head of the present genus is firm and the form is maintained in preservative irrespective of the condition of the zooids embedded in it.

The only known species of this genus is recorded from New Zealand and New South Wales.

Euclavella claviformis (Herdman, 1899)

(Fig. 27, Plate 7a–c)

Colella claviformis Herdman, 1899, p.67.
Clavelina claviformis: Kott, 1957a, p. 88. Millar, 1960, p.68; 1982, p.12.
Amaroucium anomalum Herdman, 1899, p.76.
Clavelina sigillaria Michaelsen, 1924, p.269.

Distribution

New Records New South Wales (Jervis Bay, AM Y2138; Port Hacking, AM Y2143; Port Jackson, AM Y2131; Port Stephens, QM G10152). New Zealand (Bay of Islands, QM G10155).

Previously Recorded: New South Wales (Port Jackson AM U241 U151 G12248 syntypes Herdman 1899, AM U353 holotype *A. anomalum* Herdman, 1899, AM Y1254 Kott 1957a; 11 mile S by E Ballina – AM U577). New Zealand (North Island ZMC holotype Michaelsen 1924; Millar 1960, 1982)

The species has been recorded from 15m down to 60m (AM U577).

Description

External Appearance. Colonies have a rounded to oval head up to 6cm long supported on a short, thick stalk that sometimes expands

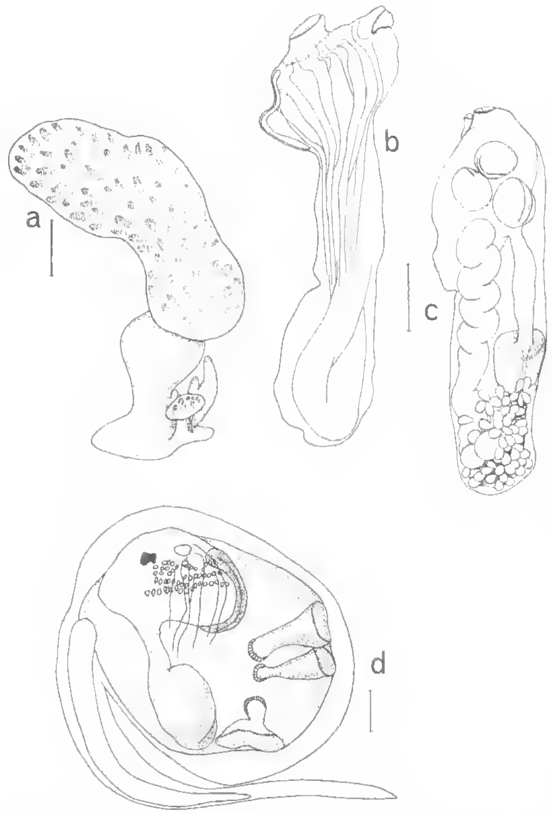


FIG. 27, *Euclavella claviformis* n.gen.: **a**, colony (QM G10152); **b,c**, zooids from right and dorsum respectively, muscles partly removed (QM G10152); **d**, larva (AM Y1254). Scales: **a**, 1cm; **b,c**, 1mm; **d**, 0.2mm.

basally to a wide and almost leathery holdfast. Otherwise the test is firm and gelatinous throughout, but firmer on the stalk than on the head. Several stalks may be joined basally. The stalk expands where it joins the head. Vascular stolons from the zooids extend down into the base of the stalk. The zooids are embedded in the head, opening all around its surface, the branchial apertures anterior to the atrial openings. Living colonies are yellow-green (AM Y2143) or opaque white with orange zooids, the colour of the zooids being apparent where their apertures project slightly from the surface.

INTERNAL STRUCTURE: Zooids are always very contracted, especially the abdomina, and their true dimensions have not been determined. Probably they are more than twice the length of most of the preserved zooids, which are never more than about 6mm. Thoracic muscles are widely spaced oblique and longitudinal bands, with formula 3E,3B,3D. However, on the abdomen they are much more numerous, completely surrounding it and obscuring the other organs. There are 3 circles of tentacles, 6 large ones in the most posterior circle; about twice the number, moderately sized, anterior to the larger ones, and in the most anterior circle a variable number of rudimentary tentacles. The neural duct opening is a small transverse oval, projecting slightly into the lumen of the pharynx.

There are 10 rows of about 40 stigmata. The stomach is about halfway down the abdomen. It probably is smooth in the living specimens, although when preserved it is collapsed into folds, apparently artefacts. The gut is no further differentiated after it leaves the stomach. It passes forward to the bilabiate anus at the posterior end of the atrial cavity as a cylindrical tube. Gonads are present in the gut loop posterior to the stomach and consist of a group of 3 or 4 small eggs surrounded by fairly numerous testis follicles which extend out over the left side of the abdomen. Up to 8 developing embryos are in a brood pouch at the postero-dorsal corner of the thorax where they appear to begin their development. They are present in colonies collected off the NSW coast (AM Y2138 Y2143) in May and June.

Larvae are large, the trunk about 1.2mm, and the tail is short, only about half the length of the trunk, although the test covering it, forming the fin, is longer (see Remarks, below). There is an ocellus but no otolith in the cerebral vesicle. No frontal plate develops, the anterior end of the trunk is unmodified except for 3 triradially arranged, tubular, adhesive organs invaginated into the body of the larva, with adhesive cells at the base of each tube. These become terminal when the tubes evert and project out in front of the larva. The bases of the inverted tubes converge in the centre of the trunk, near the developing oesophageal region.

REMARKS: Despite the wide geographic separation between the New Zealand populations and those on the central eastern coast of Australia, the only difference found in either colonies, or zooids or larvae is that the New Zealand specimens have a longer larval tail than the Australian ones. At this stage, without further differences separating them, they are considered conspecific. The colonies appear closer to *Clavelina* than to any other known genus, but they are readily distinguished by the firm test of the head in which the zooids are embedded, by the strong abdominal musculature of the zooids, and by the remarkable adhesive organs of the larvae, which were completely misinterpreted when the material was examined initially (Kott 1957a).

Family HOLOZOIDAE Berrill, 1950

Colonies are soft and fleshy, either with a thick stalk or forming sessile cushions or sheets. Zooids are completely embedded, and arranged in colonial systems which, with the exception of *Sigillina* and *Polydistoma* n.gen., are highly organised cloacal systems. Branchial openings are 6-lobed. Atrial apertures are either 6-lobed or large, plain-rimmed openings with an anterior lip. Thoraces are short, usually with 3 or 4 rows of stigmata, but occasionally with 5 or 6. Longitudinal thoracic muscles are present, but they do not always extend onto the abdomen. Oblique and transverse muscles are not always present. The gut loop is relatively short, the oesophageal neck is never long, and with few exceptions the stomach is halfway down the abdomen rather than at the posterior end as in Clavelinidae, Pycnoclavellidae and Polycitoridae. The anus opens some distance up the branchial sac. Posterior vascular processes of the zooids extend down into the stalk (when present) or into the centre or base of the colony. They do not branch, and each has either an ectodermal or an endodermal (epicardial) rather than mesodermal septum. The posterior abdominal stolon is short and inconspicuous only in the relatively thin, investing colonies of *Sigillina fantasiana*.

Gonads are contained either in the gut loop, or in a posterior abdominal sac connected to the zooid by a narrow neck, or they spill over behind the gut loop into the top of the vascular stolon. In many species large, pyriform testis follicles are arranged in grape-like clusters, but in certain *Sycozoa* and *Distaplia* only 4 to 6 long follicles are arranged parallel to one another to form a barrel-shaped mass with the short vasa efferentia joining the vas deferens at one end. The ovary is relatively small, producing few, but large eggs. In a few species (certain *Hypodistoma* and *Polydistoma* n.gen., and *Distaplia retinaculata* n.sp.) unusually large eggs are probably fertilised at the base of the oviduct and rupture into the test (where the embryos complete their development) directly from the abdomen. In all other known species eggs are fertilised and embryos incubate in a brood pouch formed from a loop of the distal part of the oviduct which projects from the postero-dorsal corner of the thorax. Larvae are large. In all genera except *Sigillina* and *Hypodistoma* adhesive organs are triradially arranged, 2 dorsal and one ventral, at the anterior end of the trunk. They consist of a relatively deep epidermal cup surrounding a deep axial cone with a hyaline cap (see Cloney 1977). In *Sigillina* and *Hypodistoma* there are 2 or 3, more complex compound adhesive organs in the median line. In *Sigillina mjöbergi* the adhesive organs are inverted tubes, as in the Pynoclavellidae and *Euherdmania*.

Replication is by horizontal division of isolated vegetative stolons which contain a tubular septum that is epicardial in origin. It is a prolific process, and the small, non-functional replicates can be seen moving up from the top of the stalk or base of the colony to take their places as functional zooids at the surface. Blastozooids also form from the epicardial tube in the oesophageal region in larvae of *Hypsistozoa* (see Brewin 1959), *Distaplia* and some *Sycozoa*.

The structure of the vascular appendages and the process of replication in *Sycozoa* has been investigated by Caullery (1909), Beneden and Selys Longchamps (1913) and Salfi (1925a, 1926); and in *Distaplia* by Kowalevsky (1874), Salensky (1893), Salfi (1925b, 1928, 1933) and Berrill (1935b, 1948b). Brien (1948) summarised their findings. In all cases, there is an ectodermal vascular process, usually consisting of two channels, that projects posteriorly from the left side of the posterior end of the abdomen. In *Distaplia* there are numerous short vegetative stolons (stolons prolifères: Brien 1948), containing a part of the left epicardial sac. These become isolated from the zooid at the posterior end of the abdomen near the vascular process but independent of it. In *Sycozoa*, long vegetative stolons, that occupy the stalk of the colony, divide progressively from their anterior to posterior ends in a prolific replicative process. These stolons contain an epithelial tube that Brien (1948) thought epicardial although Caullery (1909) was not sure of its origin. Berrill (1935b) identified, in *Distaplia magnilarva*, a further replicative process in which the remnants of the anterior tips of the epicardial tubes generate buds following resorption of the zooids. It is a process more or less homologous with the replicative process in the larvae.

Sigillina and *Hypodistoma* differ markedly from *Sycozoa* and *Distaplia*, in having a single posterior abdominal process. Like the vegetative stolon of *Sycozoa* it contains an epicardial sac (Caullery 1909; *Sigillina grandissima*, below). Although the vegetative process of *Sigillina* has not been investigated, this posterior abdominal process provides the site for a process of replication similar to that known for *Sycozoa* (see Caullery 1909). Colonies of all the stalked species of *Sigillina* examined in the present study have replicated zooids being added to the colony at the top of the stalk, and, in some cases, isolated buds are present in the stalk. This would be compatible with the production of replicates by horizontal division of the isolated vegetative stolon, as is characteristic of *Sycozoa* and *Distaplia*, thus confirming Caullery's (1909) observations on *Sigillina australis*.

As a result of his observations, Caullery (*loc. cit.*) believed *Sigillina* a member of the same family (Distomidae Giard, 1872 = Polycitoridae Michaelsen, 1904) as *Sycozoa* and *Distaplia*. Michaelsen (1930) characterised the genus *Sigillina* (in Polycitorinae of Clavelinidae) as species with 3 rows of stigmata and embedded zooids. He divided the subfamily into 5 subgenera, 2 of which (*Sigillina* and *Hyperiodistoma*) are included in the genus *Sigillina* as defined in the present work. The stomach folds that Michaelsen used to separate the subgenera *Sigillina* and *Hyperiodistoma* were probably artefacts and their presence cannot be confirmed in the Australian material. Kott (1967), basing her arguments on the larvae, assigned certain *Sigillina* to *Atapozoa* Brewin, 1956a and, on the basis of the brood pouch and the vegetative stolon, assigned the genus to Holozoinae. It is now clear that *Atapozoa* is not distinct from *Sigillina*.

The intrageneric relationships in these 2 groups of holozoid genera (characterised by differences in their vegetative stolons) are reflected in other characters. Relationships between *Sycozoa*, *Distaplia* and *Hypsistozoa* are close, all having separate vascular and vegetative stolons, cloacal systems, similar short zooids, and larvae with triradially arranged adhesive organs. *Sigillina* and *Hypodistoma* are readily separated from the 3 former genera by their single posterior abdominal stolon, 3 rather than 4 or more rows of stigmata, a 6-lobed atrial aperture, and large larvae with complex everting adhesive organs that are not obviously related to those of the other group of genera. Of the new genera described hereunder, *Neodistoma* n.gen. appears related to *Distaplia*, and *Polydistoma* n.gen. has the 6-lobed atrial apertures and short zooids with posteriorly oriented atrial siphons and horizontal gut loop of *Hypodistoma*. *Hypsistozoa* and *Neodistoma* always have a gastric reservoir in the duct of the gastro-intestinal gland. Many *Distaplia* species do too, and although *Sycozoa cerebriformis* is the only species of *Sycozoa* to have one, the fact that it occurs at all is further evidence of the differences between the 2 groups of genera in the Holozoidae. It is possible that their differences may be found to justify the erection of a new family to accommodate the *Sigillina* and related genera separately from the Holozoidae.

The genus *Hypodistoma* Tokioka, 1967a, with type species *Hypodistoma deerratum* (Sluiter, 1895), was erected to accommodate species with cloacal systems and small zooids with posteriorly directed atrial apertures and small abdomina distinguishing them from *Sigillina*. A relationship (based on larvae) exists between *H. deerratum* and related species that have cloacal systems, and *S. fantasiana* and similar species that do not. However the separation of *Hypodistoma* from *Sigillina* is supported by the small zooids of *Hypodistoma* with their posteriorly oriented atrial apertures and short abdomina, by certain differences in the larvae (see *Hypodistoma* below), and by the presence of the cloacal cavity.

Like *Polydistoma*, 2 of the 3 known species of *Hypodistoma* (*H. mirabile* and *H. vastum*) have especially large larvae that incubate in the test following rupture from the abdomen. This occurs also in *Distaplia retinaculata* n.sp., and is convergent, related to the size of the egg relative to the zooid, rather than an indication of phylogeny.

Many authors have discussed the possibility that *Sycozoa* and *Distaplia* are congeneric (Van Name 1945, Brewin 1953, Millar 1960, Abbott and Trason 1968), however, this would deny the real difference represented by the long vegetative stolon that occurs in *Sycozoa* but not in *Distaplia*. *Sycozoa* can also be distinguished from *Distaplia* by the long, often straight-sided heads, always with a stalk which sometimes is thin and leathery rather than fleshy, and with parallel double rows of zooids. There are some species of *Distaplia*, with single double row systems of zooids and a single terminal common cloacal opening, that resemble *Sycozoa* in the arrangement of their zooids. However, in these *Distaplia*, rows of zooids continue over the top of the head while in *Sycozoa* they terminate around the margin of the top of the head which is often flat, always free of zooids, and sometimes occupied by a large terminal cavity. Except for zooids at the top of the cloacal canals which have atrial lips inserted into the rim of the cloacal apertures (see Millar 1960), the atrial lips of *Sycozoa* zooids are not as long as those of *Distaplia* and do not have the tongue-like lobes on the outer border that, in the latter species, are usually inserted into the test around the rim of the cloacal aperture. Further, in *Sycozoa* the branchial lobes are reduced and often absent altogether, there are very few and delicate body muscles, parastigmatic vessels are absent, rows of stigmata are paired, the stomach wall is smooth, there are no conspicuous divisions in the gut posterior to the stomach, there is never a rectal valve, and the replicative process is more prolific.

Characters of the larvae of *Sycozoa* that distinguish them from larvae of *Distaplia* are the particularly deep axial cone of the adhesive organs, absence of ectodermal ampullae at the base of the conspicuous, smooth elliptical stalks of the adhesive organs, and absence of a frontal plate and an ocellus. In several *Sycozoa* the larval trunk contains a long epicardial tube extending forwards amongst the adhesive organs. Although it has been proposed that *Sycozoa* are unisexual (Brewin 1953), only some species of this genus are apparently so, and in others the gonads mature sequentially as in *Distaplia*.

The affinities of Holozoidae are problematical. Polycitoridae Michaelsen, 1904 (> Distomidae Giard, 1872) combined clavelinid, polycitorid and holozoid genera in the one family which Michaelsen (1930) and Huus (1937) changed into 2 subfamilies (Clavelininae and Polycitorinae) of Clavelinidae Forbes and Hanley, 1848. Van Name (1945) included the same genera in a single family, Polycitoridae, defined as genera in which the body is divided into thorax and abdomen, with the branchial tentacles arranged in several concentric circles, without internal longitudinal branchial vessels, and with the gonads in the gut loop. Berrill (1950) accepted Michaelsen's (1930) view of Clavelininae as a distinct subfamily, and also separated Holozoinae from Polycitorinae, thus recognising three subfamilies in the family Polycitoridae. Differences in the structure of the vascular stolon, the process of replication, the organisation of the colony, the structure of the larvae, and the presence or absence of a brood pouch are the basis for the elevation of these subfamilies to full family status, *viz*. Clavelinidae, Holozoidae and Polycitoridae.

Holozoidae do not appear to have a close relationship either with Clavelinidae or Polycitoridae. In addition to their smooth apertures, unique replicative process, and lack of a brood pouch constricted off from the thorax, Clavelinidae are separated from Holozoidae by their more numerous stigmata (more rows and more per row), larger gonads, more numerous eggs and embryos, branching vascular stolons without longitudinal muscles and with mesodermal septa, and smaller larvae. Further, in the larval clavelinid, adhesive organs are smaller and have shallower epidermal cups than Holozoidae, 2 adhesive organs are ventral and one dorsal rather than 2 dorsal and one ventral as in *Distaplia* and *Sycozoa* and the adult organs (especially the gut loop and pharynx) are not so well advanced. Polycitorid genera resemble Diazonidae rather than Holozoidae in the lack of a conspicuous vascular processes, and replication by horizontal division of the abdomen. They have generally smaller embryos brooded in the atrial cavity, and not in a brood pouch as in Holozoidae. If Holozoidae comprise a monophyletic group of taxa and *Sigillina* is correctly assigned to it, a common ancestry with the Pycnoclavellidae is not precluded (see below, *Sigillina*).

The rupture of large ova directly into the test for incubation, which occurs in certain holozoid species, is universal in Didemnidae and probably results from their especially large eggs relative to the size of the zooids. Nevertheless, often there are similarities between *Hypodistoma* and *Polydistoma* (Holozoidae), and *Atriolum* and *Leptoclinides* (Didemnidae) that may not be convergent, and that suggest a possible lineage for Didemnidae. The colonial organisation of the holozoid *Polydistoma* n.gen. resembles that of the didemnid *Atriolum* Kott, 1983 in which zooids have a thoracic brood pouch and a similarly oriented atrial siphon that opens into a large concavity on the upper surface of the colony. The vascular processes also resemble the simple ectodermal processes of Didemnidae, and the zooids of all these taxa have similar small, horizontal gut loops.

Larval size and form, the small number produced per zooid, the well developed brood pouch, the relatively small zooids, the highly organised colonies and, in all but *Sigillina*, the highly organised cloacal systems suggest that members of the family have a long evolutionary history as vegetatively replicating colonial organisms.

A brood pouch to incubate the few, but large, embryos produced by each zooid represents a different reproductive strategy from Clavelinidae in which numerous, smaller embryos are brooded in each atrial cavity. However, the small number of eggs produced by each zooid is, to some extent at least, compensated for by the number of zooids produced by the prolific process of replication. Species of Holozoidae form integrated colonies in which the colonies (rather than individual zooids) are the biological units. The site of replication and the brood pouch are both isolated from the zooids and neither replication nor incubation prejudice the capacity of the zooids to continue feeding and contributing to the general operation of the colony.

Holozoidae contains 9 genera, of which *Sigillina* Savigny, 1816 and *Distaplia* Della Valle, 1881 (nomen conservandum) are well represented in Australian waters. *Sycozoa* Lesson, 1830 (including *Cyathocormus* Oka, 1912) also is represented in Australian shallow water communities and the genus is now known to be more diverse than formerly it was thought, there being 8 species recorded, 5 of them indigenous. *Sycozoa* is one of the few genera in the Australian ascidian fauna with Antarctic rather than tropical affinities. *Polydistoma* n.gen. and *Neodistoma* n. gen., described from Australian waters, appear indigenous. *Hypsistozoa* Brewin, 1953 (polytypic) previously known from the Peru-Chile Trench (see Kott 1969), and New Zealand is now known to occur in Australia. Only *Protoholozoa* Kott, 1969 from Antarctic abyssal basins is not represented in Australia.

Key to the Genera of Holozoidae

(* not recorded from Australia)

1. Atrial siphons present 2
   Atrial siphons not present 4
2. Stigmata in 3 rows 3
   Stigmata in 5 rows ...... *Polydistoma* n.gen.
3. Cloacal systems present .... *Hypodistoma*
   Cloacal systems not present .... *Sigillina*
4. Cloacal systems present 5
   Cloacal systems not present .. **Protoholozoa*
5. Rows of stigmata grouped in pairs .. *Sycozoa*
   Rows of stigmata not grouped in pairs.....6
6. Gonads present in top of vascular process ... . *Hypsistozoa*
   Gonads not present in top of vascular process 7
7. Branchial sac with 4 rows of stigmata....... .... *Distaplia*
   Branchial sac with > 4 rows of stigmata..... .... *Neodistoma* n.gen.

Genus **Sigillina** Savigny, 1816

Type species: *Sigillina australis* Savigny, 1816

Colonies are fleshy, either with a round, or conical, or long and cylindrical zooid-bearing head supported on a wide, gelatinous stalk that occasionally is joined to others basally; or they are sessile cushion- or sheet-like. Zooids open separately to the exterior or into common cloacal cavities. Branchial and atrial openings both have their borders divided into 6 more or less equal lobes. Zooids are robust, the thorax and abdomen of more or less equal length, and the stomach about halfway down the abdomen. There is always an appreciable area of unperforated pharyngeal wall both anterior and posterior to the perforated part. The anus opens a short distance up the atrial cavity. Usually (with the exception of *S. fantasiana* and *S. nigra*), longitudinal muscle bands extend from the siphons down the length of the body and some of the longitudinal fibres continue along the length of the posterior abdominal process which is often very long, extending down the stalk of the colony when one is present. This process contains the extension of the left epicardial sac. Transverse thoracic muscles are sometimes (but not always) present, mainly on the posterior two-thirds of the thorax. A brood pouch usually is attached by a narrow neck to the postero-dorsal corner of the thorax, or to the side of the abdomen. One large embryo broods at a time in all species except *S. fantasiana* which has up to 3 in a sessile brood pouch. The small and often inconspicuous ovary and numerous testis follicles are present in the gut loop. Eggs are fertilised either in the brood pouch or at the base of the oviduct. All embryos in the one colony appear to be at an advanced stage of development before testis follicles mature.

Sigillinid larvae probably are not free swimming for long, for in several cases (*S. mjöbergi*, *S. grandissima* n.sp.) the tail is withdrawn before larvae are released from the brood pouch. Although the thoracic brood pouch bends up to lie just under the surface test as the embryos mature, it is possible the large larvae are liberated through the atrial aperture as they are in *S. mjöbergi* (see below) — rather than erupting through the surface test of the colony. In those species in which embryos develop in the test, larvae probably are liberated through the surface test.

Larvae of *Sigillina* (with larval trunks from one to more than 4mm long) include the largest known in the Ascidiacea. There are 2 or 3 everting adhesive organs usually in the vertical mid-line at the anterior end of the trunk but sometimes (in *S. grandissima* n.sp.) triradially arranged. They are unusual, and especially well developed. The central protrusion of each adhesive organ is surrounded by a cup of ectodermal cells or is depressed into the larval trunk. However, rather than being an axial cone as it is in *Distaplia* (see Cloney 1977), the central protrusion is a long, oval platform or ridge. When everted the columnar cells are in compound branching groups rather than forming a compact conical or cylindrical mass of cells as in most other everting adhesive organs. The exception is *S. mjöbergi* which has 2 long invaginated tubes similar to those known in Pycnoclavellidae and *Euherdmania* but unlike those of other *Sigillina*.

Other characters of *S. mjöbergi* are so sigillinid that it is difficult to invoke convergence to explain them. A relationship between *S. mjöbergi* and

TABLE 3. Summary of Characters of the Species of *Sigillina* Recorded from Australia

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Colour (living)	Muscles (longitudinal thoracic)	Stigmata (per row)	Larval trunk (length, mm)	Larval adhesive organs (number; shape of axial platform)	Larval ectodermal processes
S. cyanea	A,tr–te	Port Jackson–King George's Sound	fleshy stalked conical to cylindrical head	indigo blue	15	30+	3.3	2;circular	?
S. australis	A,te	Montebello I.–NSW	"	orange–red	15	20	2.0	2;elongate	large rounded ampullae
S. grandissima n.sp.	A,te	Dampier Arch.–South Australia	fleshy stalked massive lobed head	pinkish-white	16	20	3.5	2–4; "	"
S. signifera	WP,tr	Cape Flattery to Rowley Shoals	flat topped, inverted cone-shaped lobes	dark blue-green zooids translucent test	25	30	3.3	2; "	"
S. fantasiana	A,te	Cockburn Sd–Gabo I.	flat-topped sheets or cushions	indigo blue	10	18	1.3	2; "	fine tentacular processes with terminal expansion
S. nigra	A,te	NSW	"	"	16	20	2.0	3; "	"
S. mjöbergi	A,tr	Port Hedland–Cockburn Snd	fleshy stalked cylindrical head	? colourless ? glassy	15	40	3.3	2; invaginated tubes	none

[1] A, indigenous; WP, western Pacific; tr, tropical; te, temperate. [2] Range given anticlockwise around the continent.

Euclavella claviformis (in the family Pycnoclavellidae) is suggested by their similar colonies and larvae. However, the latter species, like other pycnoclavellids, has smooth-rimmed apertures, numerous rows of stigmata, a number of embryos incubated in the atrial cavity, a relatively long oesophageal neck and a mesodermal septum in the vascular stolon — all characters distinguishing it from *S. mjöbergi*. An alternative hypothesis that larval adhesive organs of *S. mjöbergi* are related to those of other *Sigillina* in some way not yet evident has the tempting corollary of a common ancestor for Pycnoclavellidae and the genus *Sigillina*.

The condition of the epicardial sacs in *Sigillina grandissima* n.sp. provide further support for the suggestion of a pycnoclavellid affinity for this genus. The new species has conspicuous epicardial sacs, which are not fused. *Euherdmania claviformis* (Ritter, 1903) is the only other known species in which epicardial sacs are known not to fuse (Berrill 1936) and *Euherdmania*'s affinity with the Pycnoclavellidae is established through the similarity of its long invaginated tubular larval adhesive organs.

Species of *Sigillina* have more restricted geographic ranges than are usual in the Ascidiacea. The genus is known only from the Indian and western Pacific Oceans and 7 of the 13 known species are recorded only from Australian waters. The genus is also unusual in the number of tropical indigenous species in the Australian fauna — tropical species usually having a wider range in the Indo-West Pacific (Kott 1985). However, the occurrence of sister species in South African waters may have resulted from speciation from the tropical fauna rather than being indicative of a Gondwanaland origin.

It is probable the large larvae with their long incubation in the parent colony are not widely dispersed, resulting in the isolation and speciation of populations.

Close relationships between certain species are evident. The known species fall into the following groups:

1. *Fantasiana* group, containing *S. fantasiana* from Cockburn Sound (Western Australia) to Gabo I. (Victoria); *S. nigra* from New South Wales; and probably *S. digitata* from South Africa (see Millar 1964).

   These species all form sessile, cushion-like colonies rather than upright and usually stalked ones of other species. The two Australian species have much reduced vascular stolons without apparent muscle fibres on them. The principal characteristics of the group are found in the large larvae with long, narrow ridges of columnar cells depressed into the larval epidermis, and a waist-like constriction between the anterior adhesive apparatus and the developing oozooid with its mass of yolk. Both Australian species have a ring of unusual spike-like ectodermal processes around the adhesive organs. These ectodermal processes arise in a band from the epidermis behind the adhesive apparatus and reach the surface test around the anterior end of the larval trunk. They may be homologous with the fine tentacle-like processes found in a single circle around the adhesive organs in *Hypodistoma*.
2. *Cyanea* group, containing *S. cyanea* with a range from north-western Australia south to King George Sound on the western coast and to Arrawarra on the eastern coast; *S. australis* with a wide range around the Australian coast from the Montebello Is and south across the Great Australian Bight to Port Jackson on the eastern coast; *S. grandissima* n.sp. from the Dampier Archipelago to Cockburn Sound and the Great Australian Bight; and *S. signifera* from Rowley Shoals off north western Australia, and on the eastern coast from the Swain Reefs and to the north. The latter species is the only one in this group that is recorded widely in the western Pacific, *viz*. from Indonesia and the Philippines.

   Horizontal (transverse) muscles are absent from the thorax in several species of the cyanea group, viz. *S. australis* and *S. cyanea*. However, they are present in *S. grandissima* and *S. signifera*. The longitudinal muscles continue onto the vascular process where they usually are conspicuous. Larvae are especially large, with the secretory cells of the broad adhesive organs forming large, circular or oval platforms, and with large, wide, rounded ectodermal ampullae around the anterior end of the trunk. Probably *S. mobiusi* (Hartmeyer, 1905) from South Africa and Malagasy is a member of this group.

Only *S. mjöbergi*, with its long, tubular, larval adhesive organs; and *S. psammophorus* (Hartmeyer, 1912) from South Africa with a sandy test and 8 true stomach folds, do not have a close relative amongst the known species of the genus.

Key to the Species of *Sigillina* Recorded from Australia

1. Colony a flat investing sheet 2
   Colony not a flat investing sheet 3
2. Larval trunk 1.3mm long; colony < 1cm thick . . . . *S. fantasiana*

Larval trunk 2.0mm long; colony > 1cm thick . . . . *S. nigra*
3. Colony numerous small flat-topped lobes . . . . *S. signifera*
Colony not numerous small flat-topped lobes 4
4. Colony massive conical to lobed heads; horizontal muscles on posterior two-thirds of thorax . . . . *S. grandissima* n.sp.
Colony narrow conical to cylindrical heads; no horizontal muscles on posterior two-thirds of thorax 5
5. Thoraces transparent . . . . *S. mjöbergi*
Thoraces not transparent. 6
6. Stigmata per row about 20; living colonies orange . . . . *S. australis*
Stigmata per row about 30; living colonies blue. . . . . *S. cyanea*

There are 3 other species of this genus known from adjacent areas:

Sigillina digitata (Millar, 1962) from South Africa has massive cushion-like colonies 5 to 7cm thick. The larval trunk is probably the longest known in the Ascidiacea (Millar 1964: 4 to 4.3mm long). The larval adhesive organs and ectodermal ampullae resemble those of *S. fantasiana* and *S. nigra* from southern and eastern Australia, respectively.

Sigillina mobiusi (Hartmeyer, 1905) from South Africa, Mauritius and Malagasy, has variable, sometimes upright, stalked colonies and both longitudinal and transverse thoracic muscles. It is distinguished from *S. grandissima* n.sp. by its smaller colonies and fewer (10) branchial stigmata (see also Hartmeyer 1912; ? Millar 1962; Plante and Vasseur 1966).

Sigillina psammophorus (Hartmeyer, 1912) from South Africa has an outer layer of sand, 8 stomach folds, and its affinities are not known.

Sigillina australis Savigny, 1816
(Fig. 28. Plate 7d,e)

Sigillina australis Savigny, 1816, p. 179. Caullery, 1895, p. 832; 1909, p. 47. Michaelsen, 1930, p. 495.
Atapozoa marshi Brewin, 1956a, p. 31. Millar, 1960, p. 83. Kott, 1972b, p. 168; 1975, p. 2.

DISTRIBUTION

NEW RECORDS: Western Australia (Montebello Is, WAM 989.83; Carnarvon, WAM 765-6.83 857.83, QM GH2151 2; Houtman's Abrolhos, WAM 773.83; Triggs I., WAM 75.78 24.84 16.87 18.87 191.87; Cockburn Sound, WAM 20.84, QM G9479; Cape Naturaliste, WAM 132.75; Margaret River, WAM 778.83; King George Sound, WAM 987.83). South Australia (Great Australian Bight, QM GH944 GH947). New South Wales (Nelsons Bay, QM G9634).

PREVIOUSLY RECORDED: Western Australia (Sharks Bay to Albany — Michaelsen 1930; Triggs I. — Brewin 1956a). South Australia (Great Australian Bight — Kott 1972b; Investigator Strait — Kott 1975). New South Wales (Port Jackson — Savigny 1816). New Zealand (North I. — Millar 1960).

The species has been taken down to 20m. It appears indigenous; being recorded mostly from temperate locations. However it does extend into the tropics on the North West Shelf.

DESCRIPTION

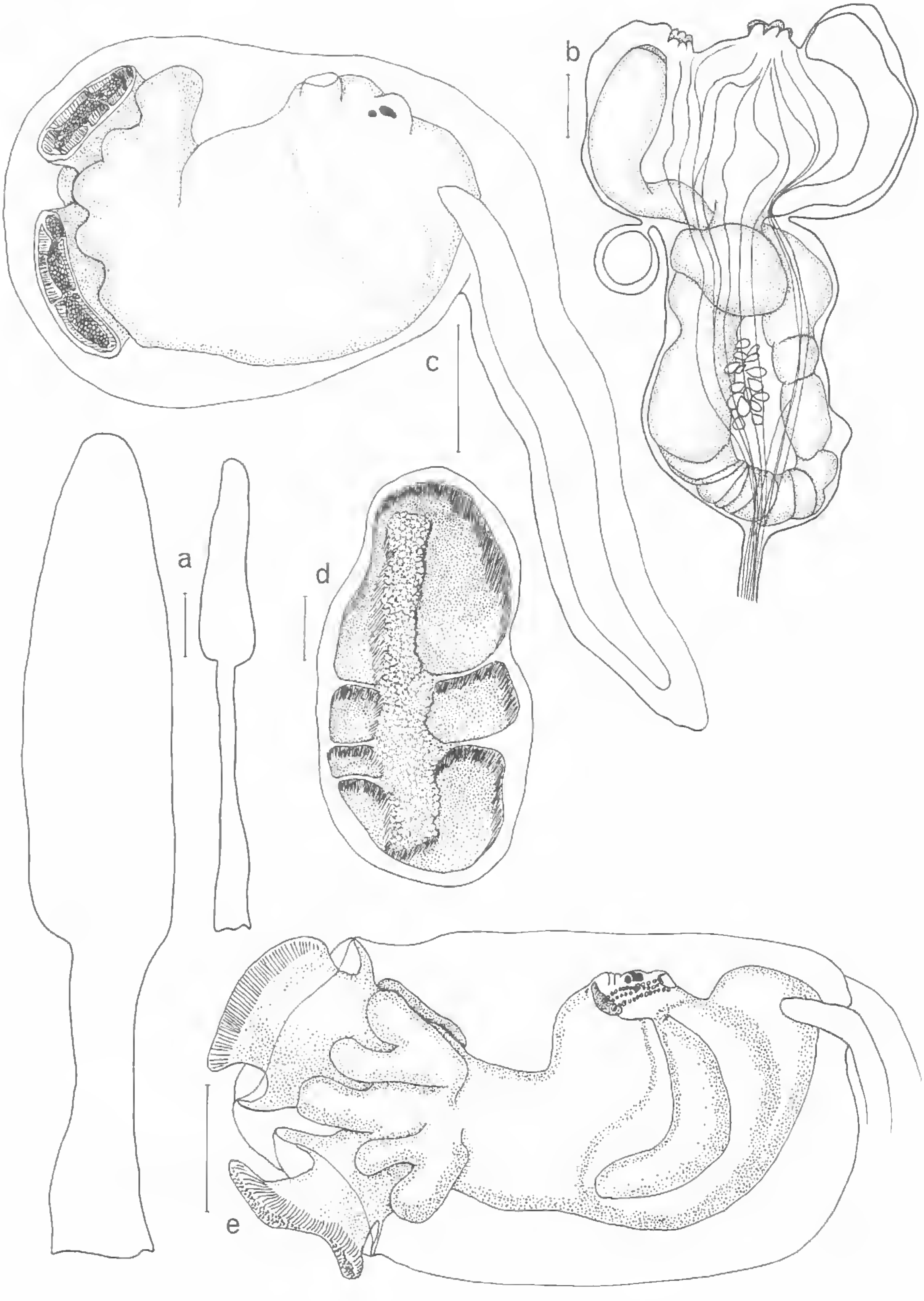
EXTERNAL APPEARANCE: The colonies are oval, or conical, or long (up to 56cm) and cylindrical zooid-bearing heads that are only slightly greater in diameter than their fleshy stalks. Stalks are longer than the head of juvenile colonies, about equal to the length of the head in moderate sized colonies, and very much shorter than the head in well developed colonies with long cylindrical rope-like heads. Zooids open all around the length of the head, the branchial aperture uppermost and the atrial aperture toward the stalk. The posterior abdominal stolons extend through the centre of the zooid bearing portion and down into the stalk. New replicated zooids are added to the colony at the top of the stalk. Zooids at the top of the zooid-bearing part are the largest and at a later stage of sexual maturity than those at the bottom.

Living colonies are orange or pinkish-orange. In preservative the test is sometimes pinkish-grey and translucent with cream to brownish zooids.

INTERNAL STRUCTURE: Zooids are about 5mm long. Thorax and abdomen are of more or less equal length, although the thorax is usually more contracted than the abdomen in the preserved material. The thorax is wide. Both apertures are on short, cylindrical siphons on the anterior end. There are about 15 longitudinal muscles on the thorax, 9 radiating from the branchial siphon and 6 from the atrial siphon. Fine circular muscles form an almost continuous sheet around each siphon, but no transverse muscles are evident on the thorax. Fine muscle bands extend from the thorax, over the abdomen and onto the long, posterior abdominal vascular stolon where they usually are conspicuous. There are about 24 branchial tentacles in 3 concentric circles, the largest in the posterior circle.

In the branchial sac there is an extensive unperforated area both anterior and posterior to the 3 rows of about 20 stigmata. Wide transverse membranes between the rows expand into triangular languets in the dorsal mid-line.

The gut loop is relatively short and straight. The small, smooth-walled stomach is in the upper third of the abdomen and there is an oval posterior


b
c
a
d
e

stomach in the descending limb. The rectum is voluminous, terminating in a smooth bilabiate anus that projects up into the atrial cavity. About 20 pear-shaped testis follicles lie in the gut loop. A small egg can sometimes be found in the oviduct. More often a single egg is found in the brood pouch attached to the postero-dorsal end of the thorax by a narrow neck. The egg is apparently fertilised, and the embryo completes its development, in the brood pouch. Eggs of zooids in each colony appear to be fertilised and development begun before testis follicles fully mature. One colony (WAM 989.83) has fully mature testis follicles and expended brood pouches. Brood pouches still attached to the dorsal border of the thorax bend up to lie just under the surface of the test as the embryos mature. Tailed larvae are present in specimens collected in December from the Montebello Is (WAM 989.83), in July from off Carnarvon (WAM 765–6.83 and 857.83), and in August from Triggs I. (WAM 16.87).

Larvae are large, the trunk about 2mm long and the tail about the same length. Developing adult organs are at the posterior end of the trunk, and a large yolk mass occupies the centre of the trunk. The anterior one-third of the trunk is taken up by the adhesive apparatus. In one colony (WAM 765.83) larvae, although they appear to be at the same stage of development, are of different sizes, ranging from 1.2 to 2.0mm. There are two long adhesive organs one above the other in the anterior mid-line. Each consists of a long strip of tall secretory cells arising from the base of a narrow trough-like depression. As the embryo develops, the larval epidermis along each side of these adhesive organs is produced into a row of 4 or 5 rounded ampullae, and each adhesive organ is produced forwards on a short wide stalk. The strip of vertical secretory cells erupts when the concave base of the trough, in which it is contained, everts, presumably as a result of internal pressure applied through the haemocoelic cavity of the larval trunk. The groups of secretory cells on their branching stalks then separate from one another to effect an attachment to the substrate over as wide an area as possible.

REMARKS. Apart from the colour of living colonies, this species resembles *Sigillina cyanea* closely and preserved specimens in which the colour is lost cannot be readily distinguished (see also Sluiter 1909, Hartmeyer 1919). *Sigillina australis* has slightly less robust zooids, with narrower thoraces and only about 20 stigmata per row, rather than the 30 stigmata per row in *S. cyanea*; and the number of testis follicles in the present species (about 20) is usually less than in *S. cyanea* (30 to 40). Further, in the latter species the test is slightly tougher, the zooids are more firmly attached to it, and the muscles on the posterior vascular stolon are more conspicuous. Clear morphological differences can be observed in larvae, those of *S. cyanea* being much larger (3mm) and having more rounded adhesive organs than the present species. *Sigillina grandissima* n.sp and *S. signifera* have similar, though even larger larvae. Specimens of the latter species are distinguished by their flat-topped, lobed colonies. *Sigillina grandissima* has distinctive granules in the epicardial endothelium, and transverse thoracic muscles.

Specimens from the type location of *Atapozoa marshi* have all the characteristics of the present species.

Sigillina cyanea (Herdman, 1899)

(Fig. 29, Plate 7f,g)

Colella cyanea Herdman, 1899, p. 70.
Eudistoma cyanea: Kott, 1957a, p. 79.
Eudistoma cyaneum: Millar, 1963a, p. 714.
Sigillina caerulea Sluiter, 1909, p. 31. Hartmeyer, 1919, p. 113.
Not *Distoma caerulea* Sluiter, 1898, p. 14.
Not *Eudistoma caeruleum*: Plante and Vasseur, 1966, p. 147. Millar, 1964, p. 163.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 986.83; Dampier Archipelago, WAM 784.83 786.83; Montebello Is, WAM 771.83 14.87; Kendrew I., WAM 976.83; North West Cape, WAM 772.83; Exmouth Gulf, QM G9480; Shark Bay, WAM 774–7.83 779.83 781.83 783.83 15.87; Cervantes I., WAM 177.87 185.87 192.87; Houtman's Abrolhos, WAM 224.88; Dongara, WAM 990.83; Penguin I., WAM 13.87, QM GH4101; Cockburn Sound, WAM 127.75 150.75 165.75 175.75 864.82 780.83 987–8.83, AM Y2132, QM G9266 G9479; Cape Naturaliste, WAM 167.87; King George Sound, WAM 19.87). New South Wales (Cronulla, AM Y2120; Nambucca Heads, QM G10008; Arrawarra, QM G9634). Queensland (Capricorn Group, QM G11906–8).

FIG. 28, *Sigillina australis*: **a**, colonies (QM GH944); **b**, zooid (WAM 75.78); **c**, early larva (WAM 766.83); **d**, adhesive organ, front view, showing central flat-topped ridge of groups of upright columnar cells. The ridge has side branches connecting it with the surrounding cup-like structure, and possibly strengthening and supporting it (WAM 766.83); **e**, advanced larva with adhesive organs everted (WAM 765.83). Scales: **a**, 1cm; **b,c,e**, 0.5mm; **d**, 0.1mm.

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Triggs I., Cockburn Sound — AM Y1280–1 Kott 1957a). New South Wales (Port Jackson — Herdman 1899). Aru Is (Sluiter 1909).

The species has been taken down to 150m. Although the records are mainly from tropical locations, especially off the northwestern Australian coast to the Arafura Sea, it also extends into temperate waters of southwestern Australia as well as New South Wales. However it has not yet been recorded from the southern coast of Australia east of King George Sound.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies have oval, conical, or very long cylindrical rope-like heads up to 70cm long and about 3cm in diameter. Fleshy stalks are almost the same diameter as the zooid-bearing head. Stalks are longer than the head when the colony is small, the same length as the head when the latter is oval or conical, but when the head is long and rope-like the stalk is very much shorter. Thus a colony of 70cm length has a stalk of only 12cm, and a colony of 7.5cm has a 5cm long stalk. Basally the stalk may separate into very short root-like projections that help it to attach to the substrate. Occasionally broad stalks are found with small regenerating heads (WAM 976.83).

Zooids open all around the head, the atrial openings uppermost and the branchial openings toward the stalk. The long posterior abdominal stolons of the zooids project into the centre of the colony and down into the stalk. The test is firm and the anterior ends of the zooids, which lie against the inside of the outer layer of test, are firmly fixed to it, and are difficult to remove from the colony.

Living colonies are indigo blue. The deep blue pigment leaches out into preservative following fixation. Colonies long in preservative have an almost colourless test and dark, or blue zooids.

INTERNAL STRUCTURE: Zooids are about 4mm long in contracted state, with the thorax only about one-quarter of the length of the abdomen. The posterior abdominal vascular stolons are particularly long and conspicuous. A layer of fine circular muscles surrounds each of the short siphons. Longitudinal thoracic muscle bands are conspicuous, about 9 radiating from the branchial siphon, and 6 from the atrial siphon. These longitudinal bands are less conspicuous over the abdomen, where they spread out rather than coalesce into a broad band. Fine muscle bands continue along the posterior abdominal stolons. There are 3 circles of branchial tentacles — about 16 in the two posterior circles and rudimentary tentacles in the anterior circle.

The pharynx is broad with 3 rows each of at least 30 stigmata. There is an expanse of unperforated pharyngeal wall both anterior and posterior to the perforated part. The oesophagus is short and the relatively small, smooth stomach is in the upper one third of the abdomen. A small, oval posterior stomach is separated from the proximal part of the rectum by a narrow constriction in the posterior third of the abdomen.

The testis, contained in the loop of the gut, consists of 30 to 40 follicles. Although a small egg is sometimes visible in the oviduct, one has not been observed in the loop of the gut, where it may be obscured by male follicles. A single, small egg apparently is fertilized and completes its development in the brood pouch which is separated from the postero-dorsal corner of the thorax by a narrow constriction. Tailed embryos are present in the brood pouches of the zooids of colonies collected in October from Cockburn Sound (WAM 988.83) and in August from Wistari Reef (QM G11908). However, well developed larvae were present only in colonies taken from Rottnest I. in January (QM G9266).

The larvae are large, with a trunk about 3.3mm long. The tail is only about the same length as the trunk. It is fusiform, narrowing to its junction with the trunk and becoming wide halfway along its length. The developing adult organs are crowded in the posterior quarter of the trunk. A large yolk mass occupies most of the trunk. Two adhesive organs are in the anterior mid-line, one above the other. Each consists of a long, vertical, oval concavity in the larval epidermis with a mass of adhesive papillae rising from the centre of the concavity. Probably as a result of pressure within the larval haemocoel the concave base of the organ everts and the papillae are thrown forward, projecting from the front of the larva, and spreading apart from one another on branching stalks. The tips of the everted papillae extend over an area of about 0.6mm diameter. An ocellus and otolith are in the cerebral vesicle.

REMARKS: *Sigillina cyanea* is mainly tropical, being absent from the southern coast of Australia, while the related *S. australis* is present across the southern coast of Australia and extends north to Port Jackson and Montebello Is on the eastern and western coasts respectively. The species overlap along the eastern and western coasts of the continent. Apart from its blue colour *S. cyanea* (especially the variations in the shape of the colonies and the morphology of the zooids) closely resembles the orange *S. australis*. However, *S. cyanea* has more numerous stigmata, more conspicuous muscle fibres on the vascular stolon

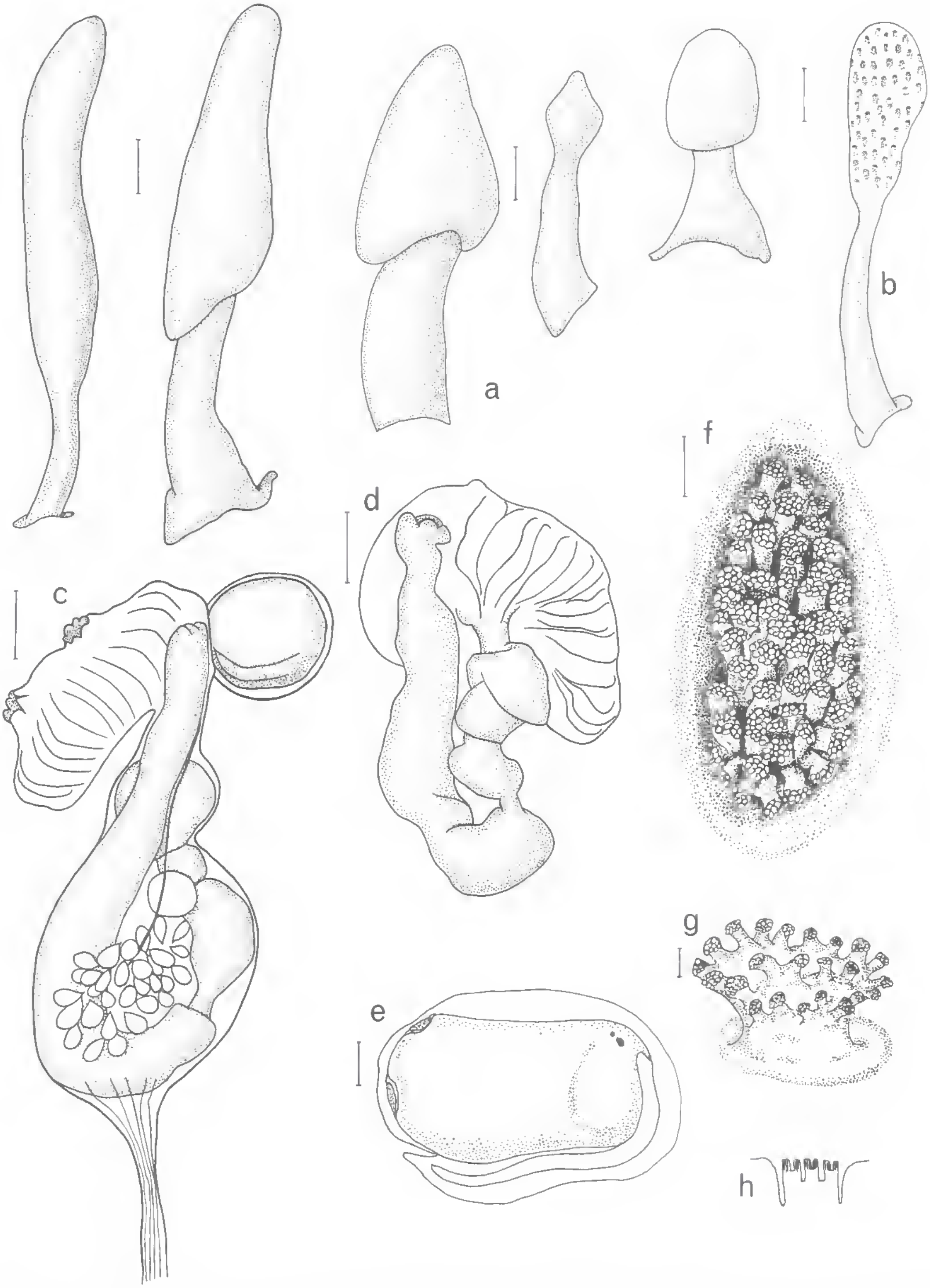


FIG. 29, *Sigillina cyanea*: **a**, outline of colonies (WAM 776.83 3x783.83 778.83); **b**, colony showing zooids (QM G9479), **c,d**, zooids from left, and postero-dorsal view with brood pouch removed (WAM 773.83); **e**, larva (QM G9266); **f**, front view of adhesive organ showing groups of columnar cells depressed into the larval ectoderm (QM G9266); **g**, everted adhesive organ (QM G9266); **h** diagrammatic section through larval ectoderm in vicinity of an adhesive organ. Scales: **a,b**, 1cm; **c–e**, 0.5mm; **f,g**, 0.1mm.

and zooids more firmly fixed in the test. Further, *S. cyanea* has a larger larva with oval groups of adhesive papillae rather than the elongate lamella of *S. australis*. As the embryos mature, the brood pouches bend anteriorly toward the atrial aperture to lie just inside the surface of the test, as in *S. australis*.

Sigillina caerulea Sluiter 1898 from South Africa, Mozambique and Malagasy is a different species — possibly of *Eudistoma* — with a characteristically eudistomid larval trunk 0.7mm long brooding in the atrial cavity (see Millar 1962; Plante and Vasseur 1966).

Sigillina fantasiana (Kott, 1957)

(Fig. 30, Plate 8a)

Eudistoma fantasiana Kott, 1957a, p. 76.
Atapozoa fantasiana: Kott, 1967, p. 187; 1972a, p. 7; 1972b, p. 168.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 863.83 *QM GH2120*, WAM 936.83). South Australia (Spencer Gulf, QM GH3704; St Vincent Gulf, SAM E2082). Victoria (Portland; Gabo I., MV F53161).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1972b; Spencer Gulf — Kott 1957a; Encounter Bay — Kott 1972a).

The species has been taken from 2 to 14m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are flat, circular to irregular investing cushions less than 1cm thick and up to 5cm in diameter with a smooth, even surface. The test is soft and, in preservative, transparent, usually with dark pigment particles, especially in the surface layers. This dark pigment is occasionally confined to the zooids themselves and is eventually lost altogether. Living specimens are bright blue throughout. Zooids are evenly spaced, opening by branchial and atrial apertures onto the upper surface of the colony. Colonies are often found growing around stems of seagrass (*Hormosira*).

INTERNAL STRUCTURE: The zooids are about 5mm long. The thorax, in moderately contracted specimens, is only about a third of the total length, the abdomen being relatively long for species of this genus. The posterior abdominal vascular stolon is relatively short and delicate, and muscle fibres were not always detected on it. About 10 longitudinal muscle bands on the thorax radiate from the apertures and posteriorly extend down each side of the abdomen, converging to a point on each side of the mid-ventral line at the level of the posterior end of the gut loop. The slender vascular stolon projects from the abdomen between the two slightly protruding points where muscles converge and terminate. There are also about 12 transverse muscle bands on the thorax. These exchange fibres with the longitudinal bands. In the branchial sac are 18 long narrow stigmata in each of 3 rows and an area of unperforated pharyngeal wall anterior and posterior to the perforated area.

The oesophagus is relatively long — the small, spherical stomach and an oval posterior stomach being present in the posterior third of the abdomen. The rectum extends from the pole of the gut loop to about half-way up the thorax. A mass of male follicles in the gut loop spread out over the left (dorsal) side of the intestine. Outside the testis follicles is a group of 3 to 5 small eggs. Eggs probably are fertilised in the upper (distal) part of the oviduct — in the upper part of the abdomen — where 3 embryos, at different stages of development can be found incubating, the most anterior being the most advanced. A marked difference in size exists between the incubating embryos in the expanded part of the oviduct (which forms a brood pouch), each successive one being about twice the size of the one posterior to it. Embyros protrude from the zooid as they develop, but the brood pouch is not constricted off from the rest of the zooid. Developing embryos are present in specimens from Cockburn Sound in November (WAM 863.83 936.83), Spencer Gulf in May (QM GH3704), St Vincent Gulf in October (SAM E2082), Wright I. (Encounter Bay, SA) in November, and Gabo I. (MV F53161) in May. In fact, the species apparently broods embryos throughout the year.

Larvae are large, the larval trunk being 1.3mm long and almost spherical. The tail is relatively long, being wound about three-quarters of the way around the trunk. Adult and larval organs are well developed with 3 rows of long stigmata, a large cerebral vesicle with ocellus and otolith and a well-formed gut loop. Two long narrow adhesive organs lie in the mid-line anteriorly. This anterior part of the larval trunk is separated from the more posterior part (containing the adult organs) by a constriction or waist. Each adhesive organ consists of a narrow, vertical strip of parallel secretory cells rising from a concavity in the anterior end of the larva. A ring of uniform, long, spike-like processes arises from the ectoderm at the base of the adhesive organs and encircles the anterior end of the larva. There are also 3 rounded ectodermal ampullae on each side, just posterior to the ring of spike-like processes, one each side of the mid-ventral and mid-dorsal lines, respectively, and one opposite the space between the two adhesive organs.

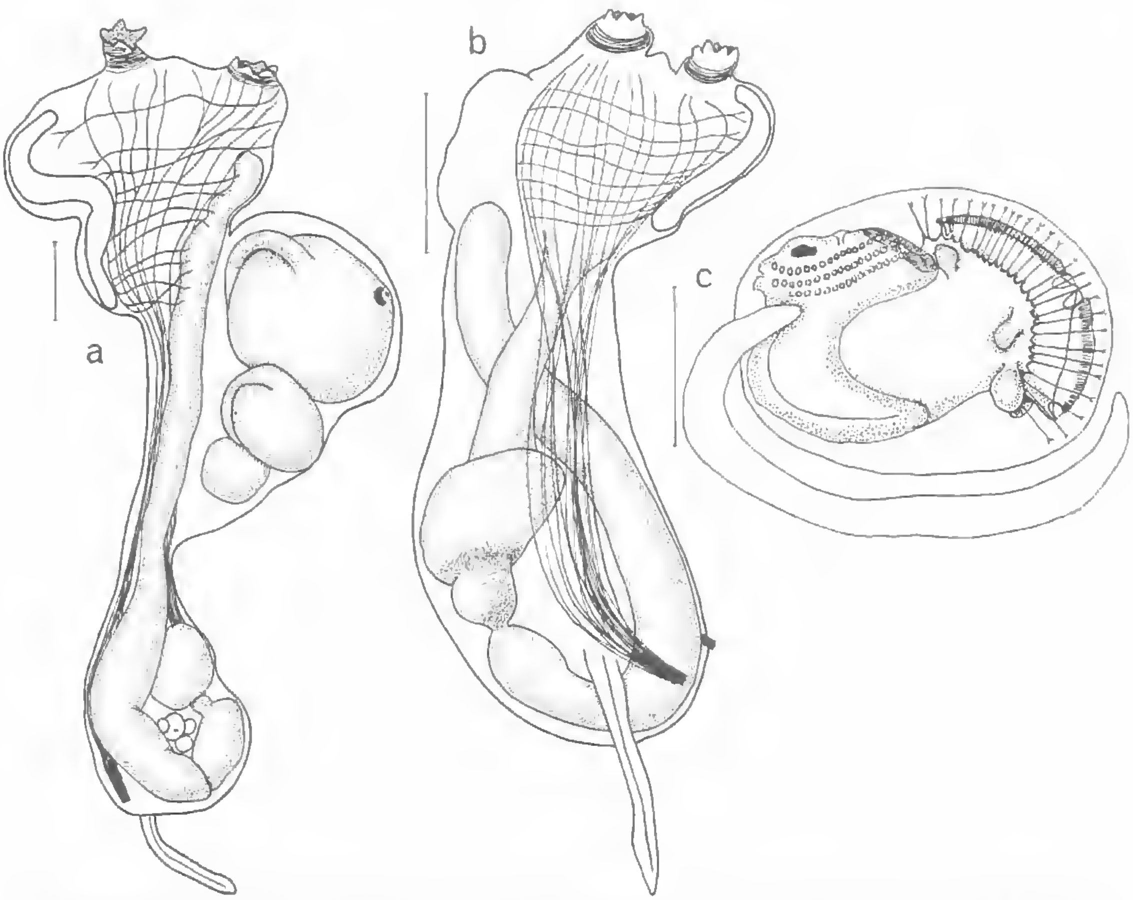


FIG. 30. *Sigillina fantasiana*: zooids, **a**, from left with embryos, and **b**, from right without embryos (QM GH2120 GH3704); **c**, larva (QM GH2120). Scales: a–c; 0,5mm.

REMARKS. This species with *S. nigra* (see below) and probably *S. digitata* from S. Africa (see Millar 1964) is a member of the fantasiana species group, characterised principally by the larvae with ectodermal spikes around the long, narrow adhesive organs, relatively small ectodermal ampullae and a waist dividing the anterior and posterior ends of the larval trunk. The fine ectodermal processes that encircle the adhesive organs are in a single ring in *S. fantasiana* but are in a wide band in *S. nigra*. These may be homologous with the ectodermal process in a circle around the adhesive organs in *Hypodistoma*. Similarly large larvae with large adhesive organs (depressed into the anterior test) occur in *Hypodistoma* although the waist is not present. The intense blue pigment in both *S. nigra* and the present species resembles that of *S. cyanea*. The colour of *S. digitata* has not been recorded.

The method of replication in this species deserves investigation, and it should be noted that accessible populations occur at 3 to 4m off Whitford Beach, Cockburn Sound, Western Australia.

Sigillina grandissima n.sp.
(Fig. 31, Plate 8b)

DISTRIBUTION

TYPE LOCALITIES: Western Australia (northwest of Rosemary I., Dampier Archipelago, 70 72m, 3.12.79, holotype WAM 846.83 *QM GH2114*; northwest of Carnac I., Cockburn Sound, 3 4m, on reef, 7.12.77, paratype WAM 782.83). South Australia (Topgallant I., Great Australian Bight, 1.7m, coll. S. Shepherd *et al.*, 29.3.82, paratypes QM GH1305, *SAM E1983*).

FURTHER RECORDS. Western Australia (northeast of Montebello Is, WAM 985.83; ?Northwest Cape, WAM 772.83; Houtman's Abrolhos, WAM 95.78 370.80 767.83 830.83 192.88 195–6.88 219.88; Cervantes I., WAM 183.87 186–7.87). South Australia (Great Australian Bight, QM GH4150).

The species has been taken from 3m down to 72m from the northwestern shelf of Western Australia and south to Cockburn Sound. Although there are no records from south of Cockburn Sound, it is probable that its range is continuous around the southwestern corner of Australia to Topgallant I. in the Great Australian Bight.

DESCRIPTION

EXTERNAL APPEARANCE. Colonies are single undivided conical to rounded lobes on short, wide stalks; or massive subdivided colonies, narrowing to a short stalk but with the individual lobes of the zooid-bearing heads tending to flatten and expand rather than narrow toward the top. Smaller lobes are rounded in section throughout, without appreciable difference in the diameter of the zooid-bearing heads and their stalks. The largest colony (WAM 846.83) is divided into 6 lobes arising from a common base: the colony is about 14cm wide and 10cm high; and the separate lobes are about 3 to 4cm diameter throughout.

Zooids, opening all around the upper half to three-quarters of each lobe, become smaller toward the base where the new vegetatively produced zooids are being added to the colony.

Living colonies from South Australia are described as bright orange zooids in a clear matrix. In preservative the zooids are often blue, although sometimes that colour is lost. The preserved test is translucent or, in a few colonies, it is hard and opaque.

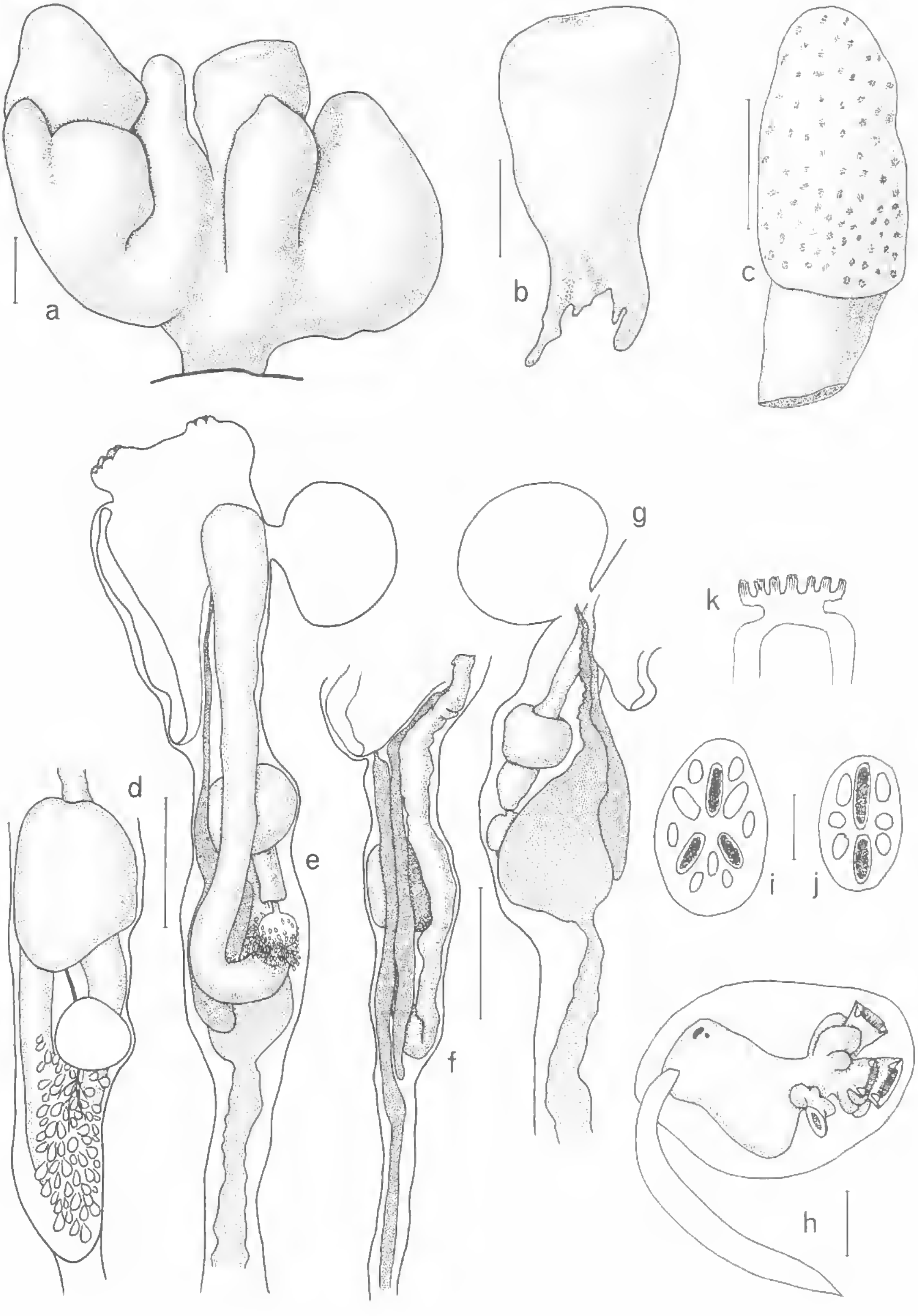
INTERNAL STRUCTURE. Zooids are about 5mm long, the thorax and abdomen of about equal length. In addition, there is a conspicuous, long and strong vascular stolon. The thorax has about 16 longitudinal muscle bands that radiate from the siphons along the length of the body, and extend onto the vascular stolon, forming a band along each side. About 10 transverse muscle bands run around the posterior two-thirds of the thorax. Eight large, but sometimes stumpy, branchial tentacles encircle the base of the branchial siphon, in front of these are 2 circles of progressively smaller tentacles. There are about 20 long stigmata in each of 3 rows, and a strip of unperforated pharyngeal wall anterior to the stigmata.

The oesophagus is about one-third of the length of the abdomen, the round, smooth stomach being in the middle third and the small posterior stomach in the posterior third. Gonads are in the gut loop and are remarkably large and conspicuous for this genus, especially the testis, which has numerous follicles spreading out over the gut. In specimens with immature testis, the male follicles can still be observed as a dense clump of follicles on the left side of the pole of the gut loop, against the rectum. A group of 2 or 3 ova lie in the abdomen. A single embryo develops in a brood pouch separated from the thorax by a narrow neck.

The most striking characters of this species are the epicardial sacs formed of dark, bluish-black, squamous epithelium, the colour derived from dark, intracellular, melanin-like granules. The left and right sacs, each with a narrow anterior horn that partly encircles the oesophagus at the posterior end of the thorax, meet, but do not fuse, ventral to the oesophagus. These sacs extend down the ventral surface of the abdomen appearing as a darkly coloured strap that protrudes into the gut loop and between the stomach and rectum. The left sac terminates blindly just posterior to the pole of the gut loop. The right sac swells out to a balloon-like expansion just posterior to the stomach, but its diameter decreases abruptly and it becomes a flattened tube at the top of the vascular process. This flattened tube forms the septum between the two blood channels along the whole length of the long, tough vascular process. In the adult zooids, the anterior horn of each sac terminates close to, but apparently does not open into, the pharynx, although it does in the larva. The dark intracellular granules are sometimes present in the endodermal cells of the pharynx, especially along each side of the endostyle and lining the stigmata. This darkly pigmented epicardial epithelium occurs in all the preserved newly recorded specimens except the holotype, in which the epicardial sacs are conspicuous and pigmented only in the larvae.

Mature larvae are present in the holotype colony (collected in December) and in a specimen from Cervantes I. (WAM 183.87) collected in May. Tailed embryos, although not fully developed larvae, are present in the Abrolhos (WAM 196.88) and South Australian specimens (QM GH1305, SAM E1983) collected in March. Larvae are robust and their test is tough and firm. The larval trunk is 3.5mm long, and the tail barely reaches to its anterior end. There is the usual otolith and ocellus in the cerebral vesicle, which is far back

FIG. 31. *Sigillina grandissima* n.sp.: a–c, colonies (holotype WAM 846.83, paratype WAM 782.83, 767.83); d–g, zooids and parts of zooids, with epicardial sacs shown in darker shadings (paratype QM GH1305 *SAM E1983*); h, larva (holotype *QM GH2114*); i,j, front view of larvae showing adhesive organs and ampullae, diagrammatic (WAM 846.83); k, diagrammatic section through an everted adhesive organ. Scales: a–c, 2cm; d–j, 1mm.


a
b
c
d
e
f
g
h
i
j
k

on the upper surface near the base of the tail. There are 2, 3 or 4 adhesive organs. When only 2, they are arranged, as in *S. australis*, in the anterior mid-line; when 3 are present they have a triradial arrangement, the dorsal one vertical in the median line and the 2 ventral ones symmetrical and radiating away from the centre of the anterior end of the trunk. A fourth, or accessory adhesive organ, is sometimes present between the symmetrical ventral ones. The adhesive organs develop in a similar way to those of *S. australis* — with the differentiation of a group of secretory cells in the base of a concavity at the anterior end of the larval trunk. In the larvae of the present species each adhesive organ, with its concavity containing the secretory cells, is produced forward on a short stalk. On settlement, the concavity everts, forcing the secretory cells forward and spreading them away from one another.

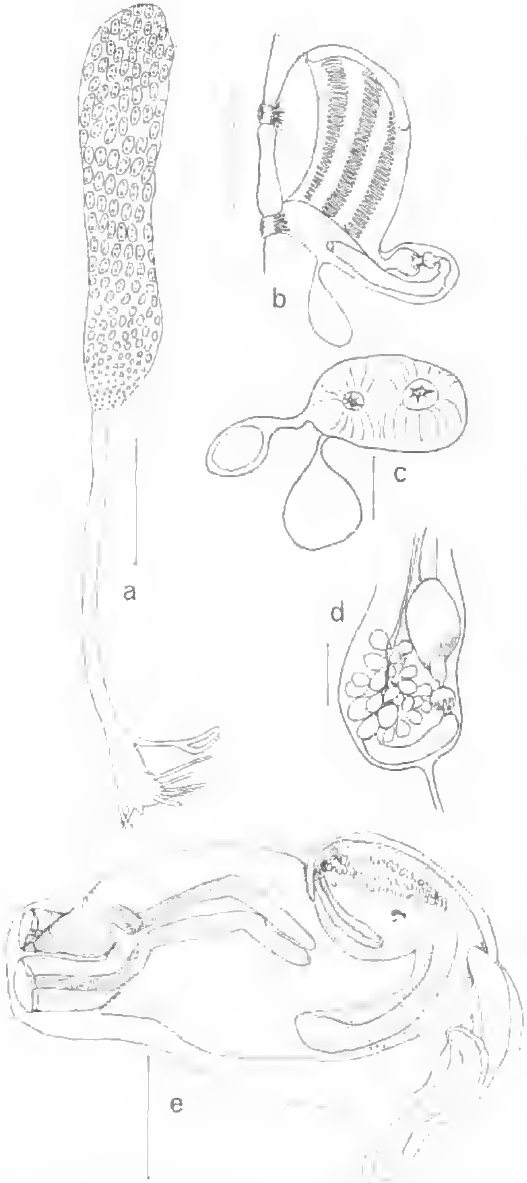


FIG. 32, *Sigillina mjöbergi*: a, colony (WAM 155.57); b, zooid showing its orientation in the colony, semidiagrammatic; c, zooid viewed from anterior end (WAM 860.83); d, abdomen (WAM 129.75); e, larva (QM GH2122). Scales: a, 2cm; b,c, 1mm; d,e, 0.5mm.

Also, large, flat, forward-projecting ectodermal ampullae are developed from the larval ectoderm around the base of the adhesive organs (as in *S. australis* and *S. signifera*). There are 3 on each side, the middle one horizontally flattened and the dorsal and ventral ones laterally flattened.

REMARKS The long vascular stolons which are sufficiently strong to be pulled from the colony without the risk of breaking, and the huge larvae (the second largest known in the Ascidiacea) are unique features of this species. The darkly pigmented wall of the epicardial cavity is also a most distinctive feature, as is the large testis with numerous follicles spreading out behind the gut loop.

Sigillina digitata (Millar, 1962) from South Africa has similar colonies to those of the present species. The South African species has smaller (3mm) zooids, shorter stigmata and larger larvae with long narrow bands of secretory cells and without the large rounded ampullae of the present species.

The affinities of *S. grandissima* are probably with the cyanea group, its larva resembling those of *S. australis*, *S. cyanea* and *S. signifera*. The orange of living colonies resembles that of *S. australis* although the blue in the preserved zooids resembles the blue of *S. cyanea* zooids that have been preserved for a long time. However, the thorax of the present species has transverse muscles — a character not shared by either *S. cyanea*, *S. australis* or *S. signifera*.

Sigillina mjöbergi Hartmeyer, 1919
(Fig. 32)

Sigillina mjöbergi Hartmeyer, 1919, p. 117.

DISTRIBUTION

NEW RECORDS. Western Australia (Port Hedland, WAM 1005.83; Dampier Archipelago, WAM 129.75 *QM GH820*, WAM 144.75; Montebello Is, WAM 860-1.83 *QM GH2122 GH2104*, WAM 991 2.83; Jurien Bay, WAM 994.83; Geraldton, QM GH4221; Dongara, WAM 993.83; Cockburn Sound, WAM 9.75 787.83).

Previously Recorded: Western Australia (Cape Jaubert — Hartmeyer 1919).

The species has been recorded down to 140m and it has not been taken from less than 30m. This may be the reason for the relatively few records and the limited known range, *viz.* the north-western continental shelf of Australia.

Description

External Appearance: Colonies consist of a cylindrical to club-shaped, glassy, transparent zooid-bearing head, not more than 6cm long and 3cm in diameter. It narrows basally to a long (up to 8cm), narrow, hard, leathery stalk that divides into root-like processes at the point of attachment to the substrate. Several heads in the present collection (WAM 860.83) do not have a stalk and, like the type material (Hartmeyer 1919), are either sessile, or have been separated from the stalk during collection. Zooids, about 4mm apart from one another, are arranged in parallel vertical rows, each zooid alternating with those in adjacent rows. As is usual for zooids in stalked colonies of most taxa, they are upside-down — the endostyle and branchial aperture below, and the dorsal border and the atrial aperture above. The thorax is perpendicular to the surface of the colony and the abdomen curves down toward the stalk. Large embryos often are present in the brood pouch lying above the zooid.

Zooids are firmly fixed in the firm test of the glassy head. Consequently they are impossible to remove entire from the colony and they do not contract on fixation. In preservative the fully expanded thoraces are clearly visible and the colonies are spectacular. The zooids become smaller toward the base of the head where new, vegetatively produced zooids are being added. The posterior vascular stolons can sometimes be seen through the hard translucent test of the stalk, but in other specimens the stalk is horny and opaque, and has barnacles, bryozoans and other epibionts growing on it.

Internal Structure: Zooids are small, not more than 4mm in total length, with the almost spherical thorax larger than the abdomen. Fifteen fine longitudinal muscle bands radiate from almost sessile, small, 6-lobed apertures, over the sides of the thorax and onto the abdomen. Some fine muscle fibres continue along the posterior abdominal vascular stolon. Branchial tentacles are arranged in 3 circles, the largest (about 8) in the outermost or most posterior circle. Thirty to 40 longish oval stigmata are in each of the 3 rows. In younger zooids it can be seen that the middle row of stigmata lengthens first, while stigmata in the anterior and posterior rows remain short and almost circular (as they are in the larvae). Stigmata in the posterior row then lengthen, first at the dorsal end of the row, while the stigmata in the anterior row lengthen first at the ventral end of the row. An area of plain unperforated membrane exists both anterior and posterior to the perforated part of the pharynx.

The gut loop is very short, with the small, rounded stomach about halfway down the abdomen. A small, oval posterior stomach is present in the descending limb. The rectum curves around in the pole of the loop and extends anteriorly to open at the base of the atrial cavity. Gonads are crowded in the gut loop, and consist of about 9 to 16 sometimes relatively large, pear-shaped testis follicles. These mature only after the single embryos in the brood pouches of most zooids in the colony are at advanced stages of development. Only one egg is present in the brood pouch at a time. It arrives there when small and, presumably, is fertilised there.

Tailed larvae are amongst the largest known in the Ascidiacea, with a larval trunk up to 3.3mm long. They are present in specimens collected off Port Hedland in October, and in April and June from the Dampier Archipelago. Specimens collected from the Montebello Is in December also have well formed embryos. Embryos at the anterior end of the colony are most advanced, or zooids there have expended brood pouches while embryos halfway along the head are reaching maturity. Despite their large size, larvae apparently are released through the neck of the brood pouch and the atrial aperture. In fact, some larvae have been found with the tail, folded back on itself, jammed into the neck of the brood pouch and the larval trunk deformed and much elongated. Others have their posterior end jammed into the neck of the brood pouch and the tail shrivelled in the process of withdrawal and resorption. Adult organs — pharynx and gut loop — are confined to the posterior end of the larval trunk. An ocellus and an otolith are in the cerebral vesicle, and 3 rows of small circular stigmata are present. Anteriorly the larval trunk is pointed, with the openings of the two long, invaginated tubes of the adhesive organs, one above the other in the anterior mid-line and a large flat, triangular epidermal ampulla on each side. Large bladder cells are packed in the larval test making it firm.

The thin invaginated tubes of the adhesive organs extend back through the larval trunk to the oozooid. As the trunk lengthens and narrows and its posterior end begins to press out into the neck of the brood pouch, the blind ends of the tubes move anteriorly, the tubes become shorter and wider. Eventually the proximal ends of the tubes (around the openings) evert slightly from the anterior end of the larva as cylindrical projections between the triangular epidermal ampullae. Subsequently the blind ends of the tubes evert and project up into the cylindrical openings at the anterior end of the larval trunk.

These large larvae are unlikely to have a free swimming phase since the tail is resorbed before their release from the parent colony. Presumably, following their release they settle down near the parent.

REMARKS: Larvae of this glassy, transparent, and possibly indigenous species are remarkable. The adhesive organs resemble those of Pycnoclavellidae and *Euherdmania*, but in the present species the long tubes have not been found completely everted before settlement. However, no other characters suggest a close phylogenetic relationship. Further, many of the characters of *S. mjöbergi* especially the single, large larva, position of the brood pouch, body musculature, 3 rows of stigmata, size of the abdomen and course of the gut are characters shared with other species of *Sigillina*.

Thus, until more evidence becomes available, the species must be considered a member of *Sigillina* in which larval adhesive organs have diverged markedly from those known in other species of the genus.

Although stalks are absent, Hartmeyer's (1919) description agrees with the recently recorded material, including the unusual pattern of development of the branchial stigmata. Stalks of this species differ from those of others in the genus, which are invariably thick and fleshy rather than narrow and leathery.

Sigillina nigra (Herdman, 1899)
(Fig. 33)

Polyclinum nigrum Herdman, 1899, p. 84.

DISTRIBUTION

NEW RECORDS: New South Wales (Bateman's Bay, AM Y2208)

PREVIOUSLY RECORDED: New South Wales (Port Jackson, AM U33 *Polyclinum nigrum* ident. Herdman, Herdman 1899).

DESCRIPTION

EXTERNAL APPEARANCE: The newly recorded colony from Bateman's Bay is robust, forming a smooth, flat sheet, up to 2cm thick, completely investing a large specimen of *Herdmania momus*. In preservative the surface layer of test is purple fading to a cloudy, white translucence toward the base. The purple is contained in spherical, fusiform and dendritic cells. The colony from Port Jackson is lumpy and potato-shaped, with clouds of black-blue pigment in the surface test (after 8 decades in alcohol preservative).

INTERNAL STRUCTURE: Zooids open separately onto the surface of the colony, and are 6mm long when moderately contracted, with the thorax from one-third to one-half of the total length. Thoracic muscles are strong, with about 16 longitudinal bands down each side, continuing along each side of the abdomen. They converge into a pointed projection on each side of the posterior end of the abdomen. There are 3 rows of about 20 long, thin stigmata. The stomach is smooth. A short duodenal area and an oval posterior stomach occur in the descending limb of the gut loop. The testis follicles are relatively large and a group of one large and 3 or 4 small oocytes lie in the gut loop. The vas deferens is conspicuous and filled with sperm in both the newly recorded specimens, collected in November and September respectively. Each has one large embryo and 2 small, non-fertile ova in a brood pouch attached to the postero-dorsal corner of the thorax and bent up against its dorsal border.

The larval trunk is 2mm long and almost spherical. The tail is wound only halfway around it. Larvae are retained in the brood pouch for a long time — being still there when the tail is withdrawn into the haemocoel and resorbed and when the adult organs are well developed. The oozooid is restricted to the posterior two-thirds of the larval trunk, which is separated from the adhesive apparatus contained in the anterior third by a waist-like constriction. However the test maintains the almost spherical shape of the trunk and is not constricted at this point. Past the waist, the larval ectoderm flares out around the 2 very long, narrow, vertical bands of adhesive cells depressed into the larval epidermis along the anterior mid-line. Most, but not all, specimens have a third, short, patch of adhesive cells, similarly depressed into the epidermis, between the 2 long bands. The whole of the anterior part of the larval trunk (with the adhesive organs) is surrounded by a band (4 or 5 deep) of fine, straight, slightly diverging, spikey tentacle-like projections that arise from the larval ectoderm just where it begins to flare. These continue through the thick larval test to its outer surface. Also, about 7 short, rather irregular ectodermal ampullae on each side project from around the waist (behind the base of the band of tentacle-like spikes). However, these are not always present — a number of well advanced larvae were found without any ectod-

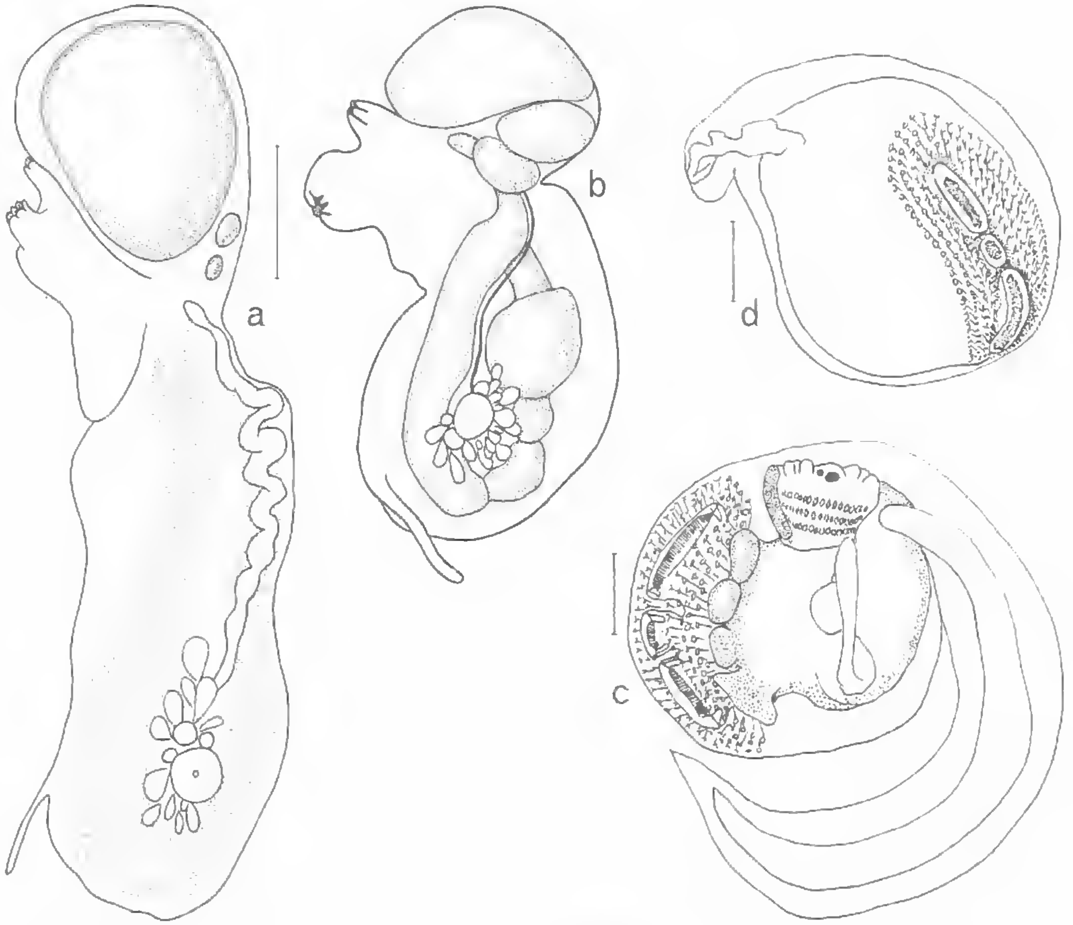


FIG. 33, *Sigillina nigra*: **a,b**, zooids (AM Y2208, holotype AM U33); **c,d**, larva (AM Y2208). Scales: **a,b**, 1mm; **c,d**, 0.5mm.

ermal ampullae. As in the larvae of *S. fantasiana* and *S. digitata*, the endostyle of the oozooid is vertical. There is dark pigment in the larval haemocoel, but not in the test.

REMARKS: The species obviously is related to *S. fantasiana*, being distinguished from it only by its larger and more robust colony and zooids, and especially by its much larger larvae and the absence of the regular paired ectodermal ampullae found in *S. fantasiana*. Clearly these large, viviparous larvae, probably without a free-swimming phase, would limit gene flow and contribute to isolation between New South Wales and southern Australian populations.

Sigillina digitata (Millar, 1962) from South Africa has a similar though even larger (4 to 4.5mm long) larval trunk than the present species (see Millar 1964). Further, the anterior end of the trunk has a similar arrangement of adhesive organs and ectodermal ampullae as *S. nigra*, although the ectodermal ampullae are longer in the South African species. Long ectodermal spikes found in both *S. nigra* and *S. fantasiana* are not recorded for the African species. However, the larvae of *S. digitata* are so large it is possible they were examined without staining and these processes may have been overlooked.

Millar (1964) speculates that the large embryo is contained in an expanded atrial cavity. However, in his specimen the brood pouch expands from the posterior end of the thorax, as in *S. nigra*, causing the thorax to be tilted at right angles to its normal orientation (see Millar 1964, p. 164).

Sigillina nigra and *S. fantasiana* are the only species in this genus to have thin vascular stolons on which muscle fibres have not been detected. It is significant that the thick (5 to 7cm) colonies of *S. digitata* have zooids with conspicuous long vascular stolons with muscle fibres on them as in other species of *Sigillina*.

Millar (1964) observed similarities between the larvae of *Hypodistoma vastum* and *H. deerratum*, and *S. fantasiana*. Larvae of the present species differ from *S. fantasiana* only in their larger size. They differ from those of *Hypodistoma* in having the adhesive apparatus separated from the posterior end of the larval trunk by a waist rather than being on a frontal plate connected to the posterior oozooid by a ventral stalk; and in having a band of spike-like, anterior ectodermal processes rather than a single ring of long, digitiform processes around the adhesive organs.

Herdman (1899) in his original description of the present species remarked on the long, narrow stigmata and the gonads in the gut loop (albeit spilling out behind it).

Sigillina signifera (Sluiter, 1909)
(Fig. 34. Plate 8c,d)

Polycitor signiferus Sluiter, 1909, p. 5.
Sycozoa sedens Sluiter, 1909, p. 34.
Eudistoma viridis Tokioka, 1955b, p. 49.
Eudistoma viride: Tokioka, 1967a, p. 122. Millar, 1975, p. 220. **Not** Nishikawa, 1984, p. 118.

DISTRIBUTION

NEW RECORDS. Western Australia (Rowley Shoals, WAM 999.83). Queensland (Swain Reefs, QM G2805–6 GH2810 GH2688 GH3805; Lizard I., QM G8595 G11902 4 G12739 GH322 GH3827 GH4096–100 GH4946; MacGillivray's Reef, QM GH4091; Cape Flattery, QM G11905; Britomart Reef, QM GH278). Philippines (QM G12755 GH411 GH451).

PREVIOUSLY RECORDED Palau Is (Tokioka 1955b, 1967a). Indonesia (ZMA TU808.1 lectotype *Polycitor signiferus* Sluiter 1909).

The species is common at shallow, sub-tidal depths in the tropical western Pacific. It is found amongst coralline algae and other weeds on hard substrates on undersides or vertical surfaces near reef edges and on the reef slope from just below low tide level down to 5m. It flourishes on the walls of channels and other locations where the current flow is fast, and where the flat, compact upper surface created by the tightly packed lobes of the colonies is advantageous.

DESCRIPTION

EXTERNAL APPEARANCE. Colonies appear as transparent bluish-green or greenish-black mats, up to 1.5cm thick, covering extensive areas. Closer examination shows these mats consist of tightly packed, separate cushion-, wedge- or mushroom-shaped, flat-topped lobes, tapering to the base which sometimes has root-like projections that help to anchor the colony. Lobes are either attached separately to the substrate or to common basal test. They vary in diameter from about 0.5cm to 3cm. Some of the more extensive plates are attached to the substrate only here and there, where the basal test grows down to form a short, irregular attachment process. Colonies are usually readily dislodged. Zooids are not crowded and can be seen opening onto the flat upper surface. The test is pale and transparent in living colonies while zooids themselves are often dark blackish-blue to bright green. Zooids become blackish-green in preservative. Green cells are concentrated anteriorly, especially in a ring around the base of the branchial siphon and in 2 symmetrical arcs, one on each side, curving down the body wall from the intersiphonal space, and in longitudinal lines on the abdomen and posterior abdominal process where they appear to be associated with the muscles. Possibly contraction of the muscles concentrates these pigment particles making them appear directly associated with the muscles. There also are some brownish-yellow and minute green pigment particles in the test of preserved specimens.

INTERNAL STRUCTURE: The thorax and abdomen together are 3 to 5mm long when contracted. In addition there is a broad posterior abdominal vascular process onto which the strong longitudinal muscles of the body wall extend to terminate abruptly at its posterior end, just before it divides into 2 or 3 short, terminal branches. About 25 longitudinal muscles are on the thorax. About 30 stigmata are in the second and third rows, with more in the first row, which inclines anteriorly along each side of the mid-dorsal line as in *Eudistoma*. Fairly extensive unperforated areas are both anterior and posterior to the stigmata.

The gut loop is short, the abdomen being only about the same length as the thorax. The stomach is spherical and smooth, about halfway down the abdomen. There is also a small posterior stomach before the tube expands into the rectum in the pole of the gut loop. Gonads, in the loop of the gut, consist of a conspicuous group of male follicles and an inconspicuous ovary. A large, tailed embryo is in the brood pouch constricted off from the postero-dorsal corner of the thorax in specimens collected in April (QM G11904), late June (QM GH4096) and December (QM GH4946) from Lizard I., and in August (QM G11805) from Cape Flattery. Specimens from the Swain Reefs had tailed embryos in July (QM GH2810) and in January (QM GH2806).

Larvae are large, with a larval trunk about 3.3mm long and a tail about the same length. Dark pigment particles occur in the larval test and an ocellus and otolith in the cerebral vesicle.

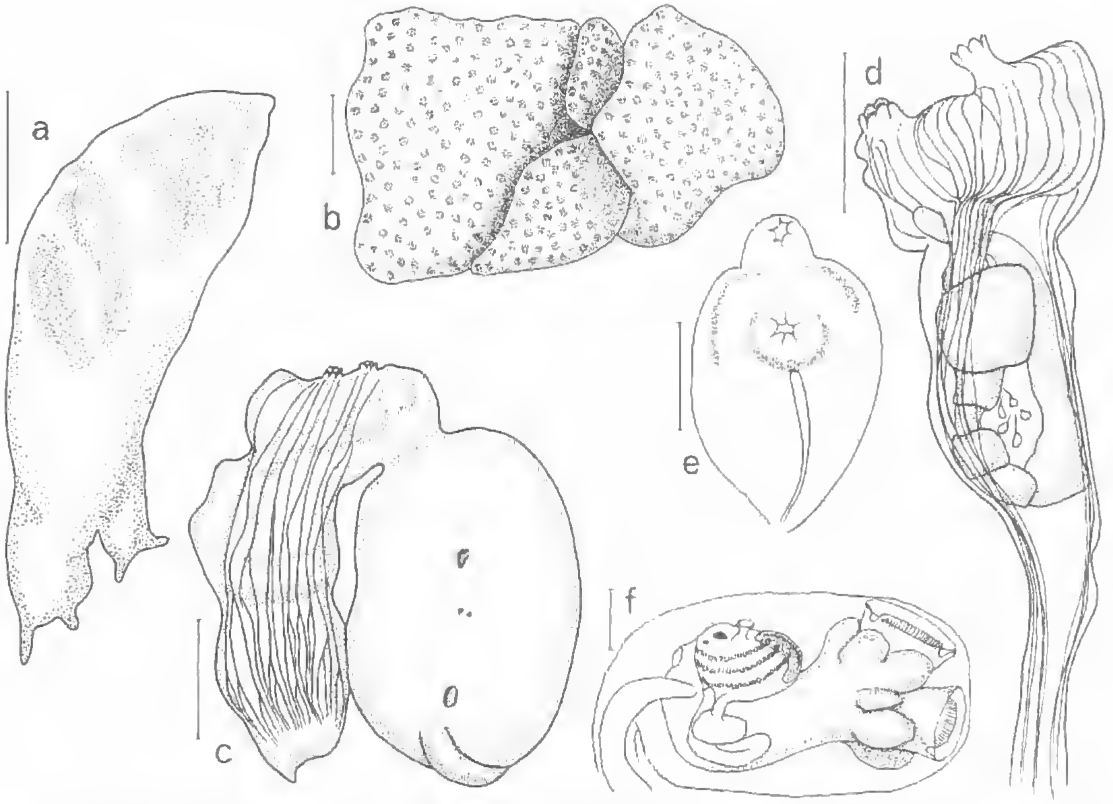


FIG. 34, *Sigillina signifera*: **a,b**, colonies (QM G11903 GH4096); **c**, contracted zooid with brood pouch (QM G8595); **d**, extended zooid (QM GH4099); **e**, thorax showing colour pattern (lectotype ZMA TU808.1); **f**, larva (QM G8595). Scales: **a**, 5mm; **b**, 1cm; **c–e**, 1mm; **f**, 0.5mm.

Two large adhesive organs are in the mid-line at the anterior end of the body. They consist of a long narrow strip of secretory cells that arise from the base of narrow depressions, and which, when the larva is mature are produced forwards on short stalks as in *S. grandissima* n.sp. Three large, forward-projecting, balloon-like ectodermal ampullae develop from each side of the trunk just posterior to the base of the adhesive organs.

REMARKS. Although the species has all of the characteristics of the genus well expressed, certain aspects of its morphology separate it from other species. These are the unique, flat-topped lobes, sometimes small and containing relatively few zooids; zooid openings on the flat upper surface; the dark colour of the zooids; and the relatively large numbers of stigmata in each row. The large larvae resemble those in the cyanea group, and in particular *S. australis*, which has 2 long adhesive organs and similar ectodermal ampullae to those in the present species. Zooids of this species also resemble those of *S. cyanea* and *S. australis* in lacking transverse muscles on the thorax.

The lectotype (ZMA TU808.1) still retains the concentrations of dark pigment cells illustrated by Sluiter (1909, pl. 1, fig. 2). These occur in many of the living as well as the preserved specimens.

Colonies of the present species resemble those of some *Eudistoma*. However, *Eudistoma* have more and smaller zooids than the present species, and never have a brood pouch nor a long posterior abdominal stolon. *Eudistoma viride*: Nishikawa, 1984 from the western Paciic with dark green test and 'roundish or flat and investing colonies' (Nishikawa 1984, p. 118), and only occasionally with a posterior abdominal stolon, are unlikely to be this species, which never has either dark green test or flat colonies.

Genus **Polydistoma** n.gen.

Type species: *Polydistoma fungiforme* n.sp.

Zooids of this genus have 5 rows of stigmata, open by a long, posteriorly directed atrial siphon onto the upper surface of the zooid-bearing part of the colony while the branchial apertures all open onto the under surface, and have a long posterior abdominal process that extends into the basal test or stalk of the colony. Fine longitudinal muscles are present on the thorax and these continue onto the abdomen and posterior abdominal process. There are 3 circles of branchial tentacles. The stomach is small, with a smooth surface, and the gut loop is short and horizontal.

The method of vegetative replication is not known, although in one species new vegetative zooids are seen being added to the system at the top of the stalk as in *Sigillina*. The assignation of the genus to the family Holozoidae is indicated by its small zooids, short gut loop, arrangement of branchial tentacles, long and conspicuous vascular process, and general resemblance to *Hypodistoma*. Further data on the method of replication is needed to confirm this affinity.

Embryos are in the available colonies of one of the species only, *viz. Polydistoma fungiforme* n.sp. They are large and probably rupture directly from the abdomen to incubate in the test as they do in *Hypodistoma* (see discussion on phylogeny of Holozoidae, above). The zooids of *Hypodistoma* are similar with small and horizontal gut loops, and long, posteriorly directed atrial siphons (although these open into common cloacal spaces rather than directly to the exterior as they do in the present genus). *Polydistoma* also differs from *Hypodistoma* in its posterior abdominal process which does not appear to have a septum, and its 5 rather than 3 rows of stigmata.

There are two recognised species in this genus, both from the southern half of western Australia. They differ from one another in the shape of the colony and in the number of stigmata in the branchial sac.

Polydistoma fungiforme n.sp.
(Fig. 35)

DISTRIBUTION

TYPE LOCALITY: Western Australia (about 27km W of Cliff Head, Dongara, 29°30′S 114°41.3′E, to 29°31.7′S 114°42′E, 44m, MV *Sprightly* 17.2.76, pipe dredge, holotype WAM 881.83; about 26km SW of Dongara, 29°23′S 114°42′E to 29°24′S 114°42′E, 33m, 17.2.76, paratypes WAM 880.83 *QM GH2111*).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of an irregularly branched cylindrical stalk (about 2cm in diameter) with each of the 3 to 6 branches terminating in a zooid-bearing saucer- to trumpet-shaped expansion or frond from 3 to 10cm in diameter. The fronds are thinner around their outer circumference than in the centre, where the under surface tapers to the stalk. Each frond is concave on its upper (free) surface. There is no indication of how the colony is fixed — there is no basal stalk and all the terminal branches have zooid-bearing terminal expansions. The long posteriorly projecting atrial siphons open onto the upper concave surface and the branchial apertures are on the under surface. The concavity is homologous with a cloacal cavity. Zooids are evenly spaced in the terminal fronds, about 2mm apart. Stalks contain long, parallel vascular processes. Smaller zooids are in the centre where the new replicates are moving up into the frond. Larger and older zooids are toward the outer margin.

In preservative colonies are all cream-coloured with orange pigment particles around the branchial apertures. Their living colour is not known. The test is firm and translucent.

INTERNAL STRUCTURE: Zooids are about 3mm long. The thorax is longer than the abdomen, the gut loop being horizontally oriented behind the thorax. The 6-lobed branchial aperture is on a short terminal siphon. The atrial aperture is on a long, narrow, posteriorly directed siphon from the postero-dorsal corner of the thorax. The atrial siphons of smaller zooids in the central (thickest) part of the colony are long (up to 4 times the length of the zooid). About 30 branchial tentacles lie in 3 circles at the base of the branchial siphon, the 16 longest being in the posterior circle. Ten fine longitudinal muscle bands on the thorax extend from the branchial siphon and onto the abdomen — where they are inconspicuous. Longitudinal muscle bands also extend along the atrial siphon, including a few from the branchial to the atrial aperture along the dorsal border of the body. The neural gland and ganglion are close together at the anterior end of the body. The opening of the neural gland is a curved slit, obliquely oriented, and directed anteriorly and to the left. It has a conspicuous tongue-like flap projecting posteriorly from the right border of the slit. Dorsal languets are rather short, triangular expansions of the transverse vessels where they cross the dorsal mid-line. There are 5 rows each of 15 long, rectangular stigmata, but no parastigmatic vessels.

The oesophagus curves toward the ventral side of the zooid, opening into a small, smooth, spherical stomach with an extremely short suture line. The stomach lies horizontally about halfway across the posterior end of the thorax. A fairly long duodenal area extends posteriorly from the stomach and curves ventrally before narrowing to a long mid-intestine that forms the pole of the gut loop. The mid-intestine has a posterior

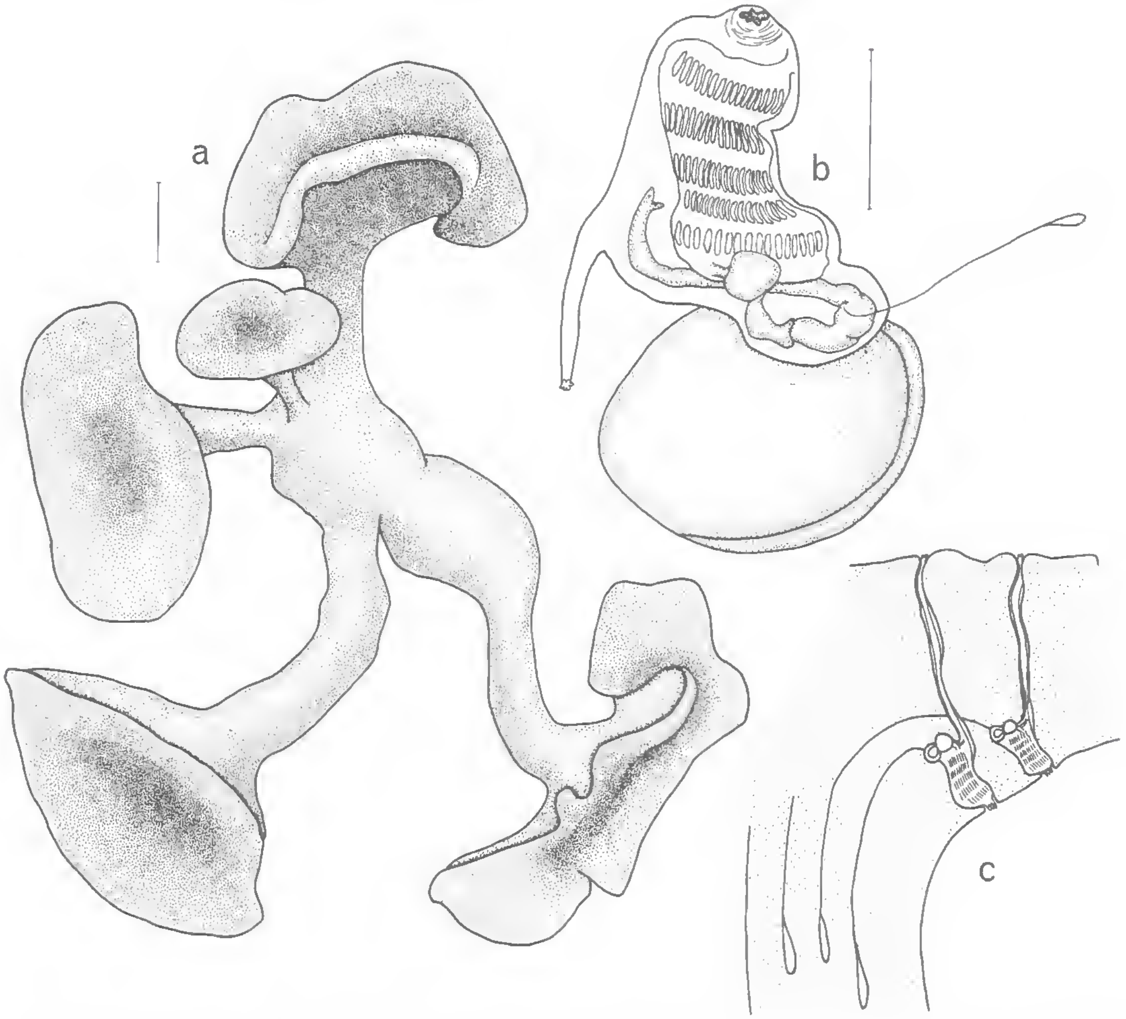


FIG. 35, *Polydistoma fungiforme* n.gen. n.sp. (holotype WAM 881.83): **a**, colony; **b**, zooid; **c**, diagram showing position of zooids in colony. Scales: **a**, 2cm; **b**, 1mm.

stomach expansion about halfway along its length. The rectum curves up to extend horizontally across the posterior end of the thorax, sometimes a little to the left. The distal portion of the rectum opens at the base of the atrial siphon in a two-lipped anus, or occasionally it is found curved over into the proximal part of the siphon. The vascular process is fine and originates from the left side of the gut loop. It has a rounded terminal ampulla. These processes are about 1mm long in zooids from the periphery of the frond, but they are long, extending parallel to one another down into the stalk in smaller zooids in the centre.

Gonads were not detected in any of the specimens. Large embryos (about 2mm long) are posterior to the abdomen, probably having ruptured from the side of the gut loop. Although the tail is differentiated in some, no other structure is discernible.

REMARKS: *Polydistoma longitube* does not have a concavity or other cloacal homologue and, although closely related to the present species, it has a vastly different colony structure. The present species appears unique, and its morphology is striking. Although there is no record of its appearance when living, it is possibly beautiful, with translucent palm-like fronds, in which the zooids are embedded. There is no sign of its point of attachment in the one available colony, but it is not impossible that has broken free — it is not likely to be planktonic.

Polydistoma longitube Kott, 1957

(Fig. 36)

Polycitor longitubis Kott, 1957a, p. 80.

Distribution

New Records: none.

Previously Recorded: Western Australia (? between Cockburn Sound and Albany — AM Y802 Kott 1957a).

Description

External Appearance: Only the holotype colony has so far been collected. It is a fleshy, circular cushion, 2cm thick and 6cm in diameter. However, the colony appears flattened, and in life it could have been upright, possibly top-shaped. The centre is firm, gelatinous, zooid-free, and has

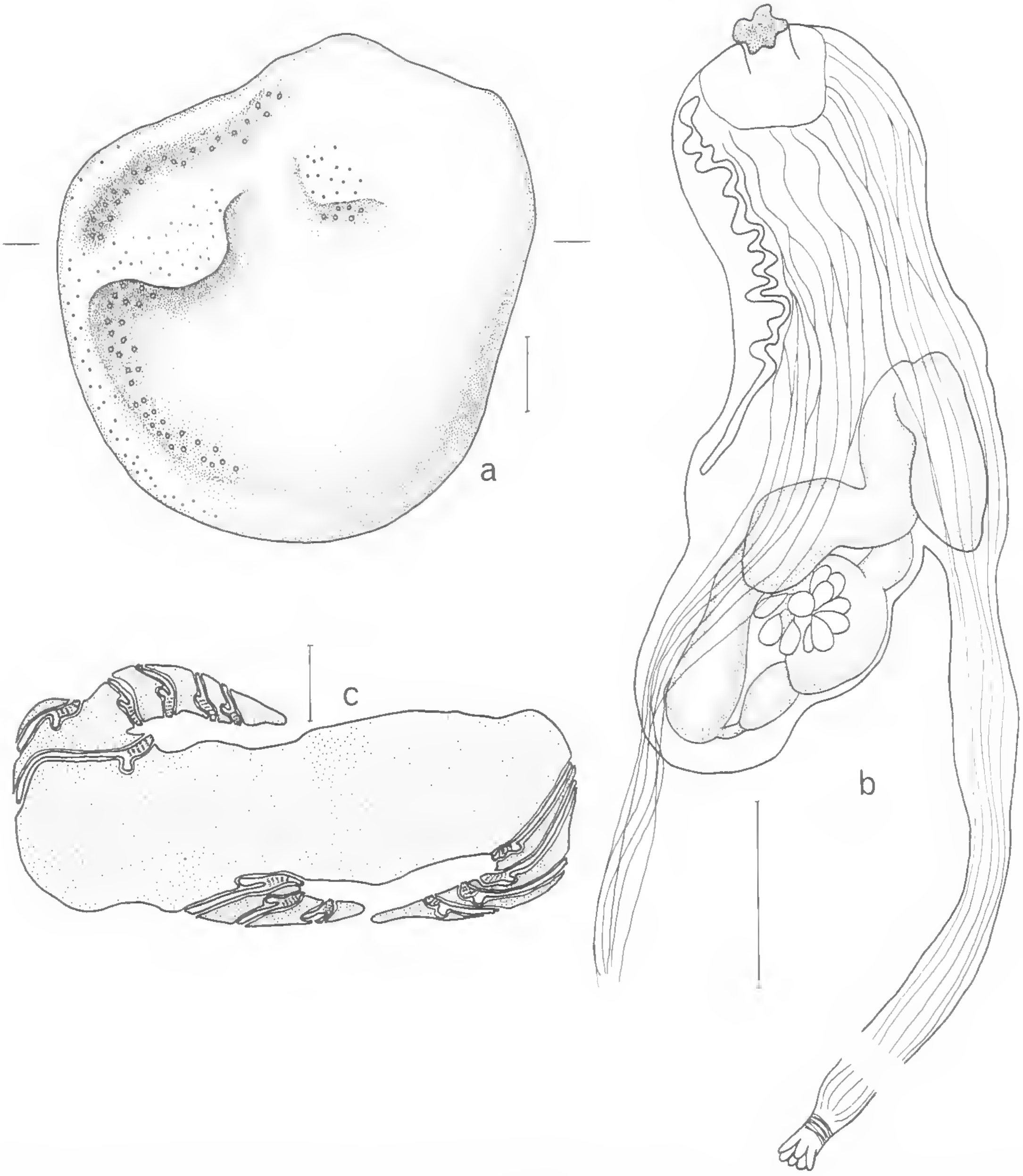


Fig. 36, *Polydistoma longitube* n.gen. (holotype AM 802): **a**, colony; **b**, zooid; **c**, diagram showing position of zooids in colony and vascular stolons reaching down into stalk. Scales: **a**, 1cm; **b**, 0.5mm.

the vascular processes of zooids irregularly scattered through it. Zooids are in the surface layer of test in areas representing about three-quarters of the upper surface of the flattened cushion. Branchial apertures of zooids around the periphery open into a depression just inside the margin of the upper surface, and their long atrial siphons sometimes extend a considerable distance through the test to open on the sides of the cushion. Zooids are also in rather, thin, irregular flaps of test that seem to overgrow the surface of the colony to form pockets. The branchial apertures of the zooids in these flaps open on the under surface of the flap into the space it encloses against the surface of the remainder of the colony. The long atrial siphons open on the outer surface of the flaps which develop from around the periphery of the colony and grow toward the centre, as well as growing over toward the periphery from the centre.

Internal Structure: Zooids are only about 2mm long. The thorax is longer than the abdomen which is folded in tightly behind the thorax. The long atrial siphon from the postero-dorsal part of the thorax is up to 1cm long, however. About 10 fine longitudinal muscles occur on the thorax, and some extend along the dorsal border of the thorax between the branchial and atrial siphons. There are 6 branchial lobes, but none were detected on the tip of the atrial siphon. Twenty stigmata occur in each of 5 rows in the branchial sac, although these were difficult to count. There are no parastigmatic vessels.

The gut is rather voluminous, with a smooth and almost spherical stomach, a long duodenal area, and a long mid-intestine with a pear-shaped posterior stomach about halfway along its length. The rectum curves up against the left side of the branchial wall before turning back abruptly so that its distal end is in the base of the atrial siphon. A circle of about 12 pear-shaped male follicles lie in the gut loop. No ovary was detected.

A long vascular process extends from the right side of the posterior end of the abdomen, and it has a few fine muscle fibres on it.

Remarks. Despite the similarity of its zooids to those of *P. fungiforme*, the present species appears distinct. *Polydistoma fungiforme* has relatively narrow cylindrical stalks with circular zooid-bearing terminal fronds that contrast with the massive central test and thin irregular flaps of zooid-bearing test of the present species.

Polycitor torosus Sluiter, 1909 has a colony that resembles that of the present species, and a long atrial siphon from the posterior end of the thorax. However, it has only 3 rows of stigmata and belongs in the new genus *Exostoma* in the Polycitoridae.

Genus **Hypodistoma** Tokioka, 1967

Type species: *Distoma deerratum* Sluiter, 1895.

Colonies are massive, soft and sessile. Zooids are small, with long, posteriorly projecting atrial siphons opening into extensive cloacal spaces which separate a basal or central core of test from the outer, zooid-bearing layer. Atrial apertures are 6-lobed. The abdomen is relatively short, usually shorter than the thorax. Fine longitudinal muscle bands on the thorax continue onto the long posterior abdominal stolons that extend into the central core of test. On the thorax transverse muscles lie beneath the longitudinal ones. There are 3 rows of stigmata, without parastigmatic vessels.

Ova probably are fertilised in the abdomen. Sometimes embryos are incubated free in the test having detached themselves from the abdomen (*H. vastum*, *H. mirabile*); or they develop, one at a time, in a brood pouch attached to the postero-dorsal corner of the thorax (*H. deerratum*).

Larvae, known for all except *H. mirabile*, are large and have an unusual fringe of uniform tentacle-like processes around the characteristic adhesive organs. The adhesive organs are depressed into a frontal plate which is joined to the posterior half of the larval trunk by a ventral stolon.

The similarity between the larvae of this genus and those of *Sigillina* may be only apparent, associated with their large size. The adhesive organs are large and depressed into the ectoderm in both species. However, in *Sigillina* a waist separates the anterior adhesive region of the larval trunk from the posterior half with its developing blastozooid, while in *Hypodistoma* the adhesive organs are on a frontal plate that is joined to the posterior part of the larval trunk by a ventral stolon. The spike-like processes that radiate out through the test from the anterior part of the larval epidermis in *Sigillina fantasiana* and related species may be homologues of the ring of tentacle-like processes that surround the adhesive organs in *Hypodistoma* — but that is not certain. The presence of 3 rows of stigmata, in *Hypodistoma* and *Sigillina* could be a convergent character, as zooids of *Polydistoma* n.gen., with more rows of stigmata, are otherwise more like the zooids of *Hypodistoma* than *Sigillina*. *Hypodistoma* also resembles the new genus *Polydistoma* in that fertilisation is probably at the base of the oviduct,

TABLE 4. SUMMARY OF CHARACTERS OF THE SPECIES OF *HYPODISTOMA* RECORDED FROM AUSTRALIA

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Systems	Larval trunk (length, mm)	Incubation of embryos
H. mirabile	A,te	South Australia	irregular cushion	numerous scattered cloacal apertures	?	? separated from abdomen
H. deerratum	WP,tr	Low Is–Abrolhos	flask	single terminal cloacal aperture	0.8	in thoracic brood pouch

[1]A, indigenous; WP, western Pacific; tr, tropical; te, temperate. [2]Range given anticlockwise around the continent.

the embryos separating from the abdomen and developing in the test (see discussion on Holozoidae, above).

Hypodistoma vastum: Tokioka, 1967a was thought a synonym of *H. vastum* (Millar, 1962). However, Tokioka's specimen lacks the large posterior abdominal stolon, has the long zooids characteristic of *Polycitoridae* and is a junior synonym of *Polycitor ianthinus* Sluiter, 1909 (see Millar 1975). It has been assigned to the new genus *Exostoma* in the Polycitoridae (see below).

Hypodistoma is represented by 3 species, *H. deeratum* from the Philippines to Houtman's Abrolhos on the western coast of Australia and Heron I. on the eastern coast, *H. mirabile* from the Great Australian Bight to Western Port (Victoria), and *H. vastum* Millar, 1962 from South Africa (see also Millar 1963b). It appears an Indo-West Pacific genus, *H. vasta* and *H. mirabile* being temperate representatives.

The species are distinguished from one another by differences in colony form, by differences in the size of the larvae, and by differences in brooding of the embryos — *H. vastum* and *H. mirabile* have embryos incubating in the test, having separated from the abdomen, while those of *H. deerratum* move from the abdomen into a narrow-necked thoracic brood pouch.

Hypodistoma vastum (Millar, 1962) from South Africa (see also Millar 1963b, 1964) resembles *H. deerratum*, and its relationship with the latter species is discussed below (see *H. deerratum*).

Hypodistoma deerratum (Sluiter, 1895)

(Fig. 37. Plate 8e)

Distoma deerrata Sluiter, 1895, p. 167.
Sigillina deerrata: Hastings, 1931, p. 87.
Atapozoa deerrata: Kott, 1967, p. 185; 1972e, p. 44.
Hypodistoma deerrata: Millar, 1975, p. 215.
Polycitor coalitus Sluiter, 1909, p. 23.
Sigillina (*Polycitor*) *coalita*: Michaelsen, 1930, p. 484.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 995.83 997.83; Cape Preston, WAM 791.83; Montebello Is WAM 789.83 998.83; Dampier Archipelago, WAM 996.83; Houtman's Abrolhos, WAM 788.83 790.83). Queensland (Heron I., QM GH1383; Abbot Point, QM GH706 GH729; Townsville, QM G8590; Cairns, QM GH4095; Lizard I., QM G10153, AM Y2134; Stanley Reef, QM GH2351; Cape Tribulation, QM GH781, AM Y2140; Cape Kimberley, QM GH4092; Princess Charlotte Bay, QM GH4094; Bathurst Head, QM GH4093; Thursday I., QM G9809–11 GH301; Murray I., QM GH301). Northern Territory (Darwin, QM GH 4225).

PREVIOUSLY RECORDED: Queensland (Low Is — Hastings 1931; Thursday I., Torres Strait — Sluiter

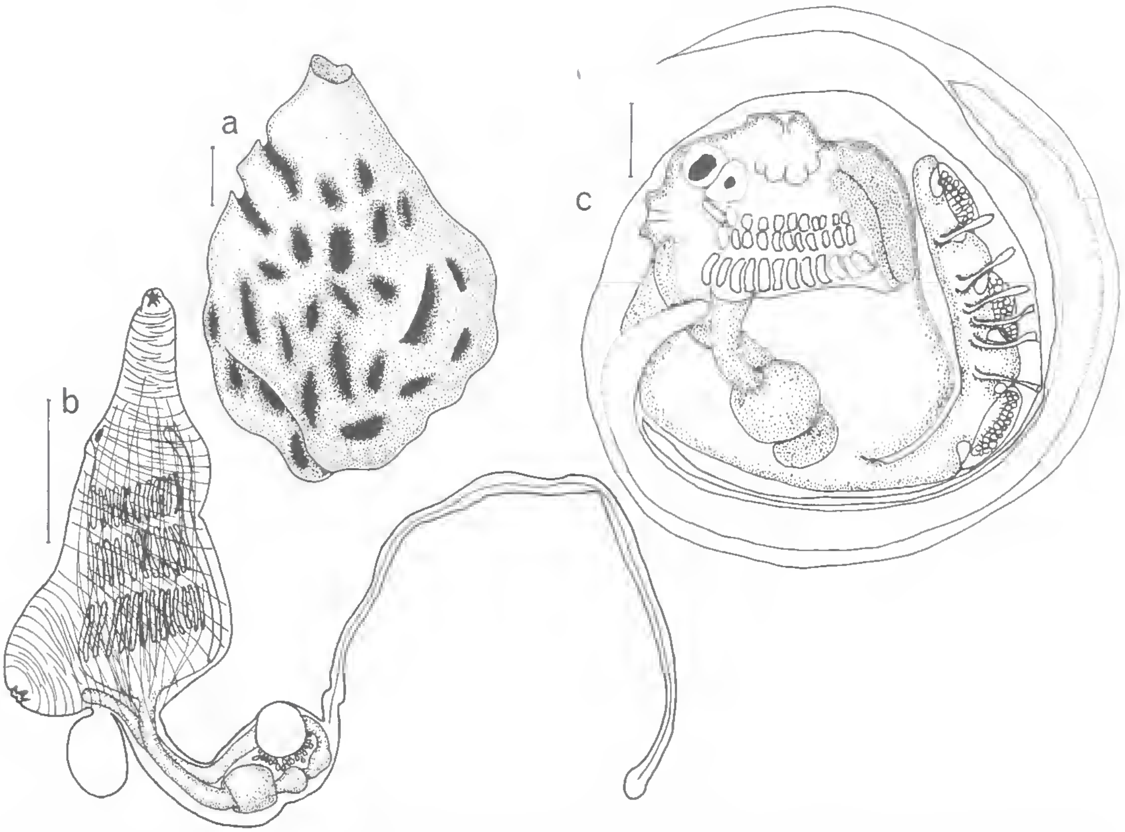


FIG. 37, *Hypodistoma deerratum*: **a**, colony (QM GH2354); **b**, zooid (QM G10153); **c**, larva (WAM 791.83). Scales: **a**, 1cm; **b**, 1mm; **c**, 0.1mm.

1895). Northern Territory (Gulf of Carpentaria — Kott 1966, 1972e). Philippines (Millar 1975).

The species has been recorded down to 80m. It is tropical, extending south only to Houtman's Abrolhos and Heron I. — the southern extent of the coralline regions on the western and eastern coasts of Australia, respectively.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are large (up to about 15cm high and 8cm diameter) upright and more or less flask-shaped, narrowing to a firm base and often narrowing terminally as well. A large, often terminal, cloacal aperture, surrounded by thin zooid-free test, has a smooth rim and protrudes from the upper surface. The firm basal test continues up into the centre of the colony forming a firm core. The outer layer of zooid-bearing test, which often continues above the central test core to enclose a central cavity in the upper part of the colony, is soft, irregular and complex, being divided by deep furrows that separate the surface into lobes and ridges. It is penetrated by large cloacal spaces that partially separate the zooid-bearing layer from the central core of firm test. Zooids are crowded in circular groups beneath the outer surface of the test as well as in the base of the furrows and clefts in the surface. Branchial apertures open to the surface where the zooids are located. Atrial apertures are on long, tubular siphons that open into the large cloacal spaces behind the zooids. The circular areas containing the zooids often protrude as shallow mounds from the surface of the colony.

In preservative colonies are rather dirty beige, pink or purple, sometimes with brown flecks. Living colonies have been described as 'grey with yellow' and 'purple variegated'.

INTERNAL STRUCTURE: Zooids are small, about 3mm long, excluding the siphons. The branchial siphon is sometimes as long as the rest of the zooid. The atrial siphon, projecting posteriorly from the posterior end of the dorsal border of the thorax, is at least as long as the branchial siphon, but often it is longer. Both apertures have 6 small lobes around their rims. A long, narrow posterior abdominal stolon extends from the posterior end of the abdomen into the central test core of the colony. The thorax has circular muscle fibres forming an almost continuous coat around its posterior two-thirds. The siphons are also surrounded with circular muscles. Longitudinal muscle bands from each siphon extend along the length of the abdomen. About 6 fine muscle fibres are on the posterior abdominal stolon.

The branchial sac has 3 rows each of 10 long stigmata. A wide expanse of unperforated pharyngeal wall lies anterior to the stigmata and another less wide is at the posterior end of the pharynx. The abdomen is shorter than the thorax and the gut loop tight and rather narrow. The small, spherical stomach is in the posterior third of the descending loop. Thus, the oesophagus is longer than it usually is in *Sigillina*. There is a small, oval, posterior stomach in the descending limb before the gut expands into the rectum. Gonads, in the abdomen, consist of a small group of testis follicles, and usually one large ovum. Embryos develop, one at a time, in the brood pouch separated from the postero-dorsal corner of the thorax by a narrow neck. Tailed larvae are in the brood pouch in some specimens taken from Cape Preston in December (WAM 791.83), from Lizard I. in November (QM G10153), from off Cairns in February (QM G4095), and from off Cape Tribulation (QM GH781) and Cape Kimberley (QM GH4092) in September.

The larval trunk is more or less spherical, 0.8mm in diameter. The tail is wound three-quarters of the way around the trunk. Most of the larval trunk is occupied by the developing adult organs, *viz.* the pharynx with its 3 rows of stigmata and the developing gut loop. The three adhesive organs are in the median vertical line at the anterior end of the trunk. They are carried on a stalked frontal plate that extends dorsally from the ventral part of the anterior end of the oozooid. Each consists of a central column of adhesive cells rising from the base of a concavity in the epidermis of the frontal plate. There is a large ocellus and an otolith in the cerebral vesicle. A fringe of evenly spaced, parallel, forward-projecting, fine, tentacle-like projections of uniform length encircle the frontal plate reaching from the base of the adhesive organs to the surface of the test.

REMARKS: The South African *Hypodistoma vastum* (Millar, 1962) is distinguished from the present species mainly by its larger larva (the larval trunk being 1.9mm long). The embryo apparently separates from the abdomen and develops free in the test rather than in a brood pouch attached to the thorax (Millar 1963b). *Hypodistoma mirabile* is distinguished by its cushion-like rather than upright colonies, the longitudinal ridges on its surface, its longer (7mm) zooids, and (like *H. vastum*) the absence of a thoracic brood pouch.

Hypodistoma mirabile (Kott, 1972)

(Fig. 38, Plate 8h)

Atapozoa mirabilis Kott, 1972b, p. 168; 1976, p. 56.

DISTRIBUTION

NEW RECORDS: South Australia (Great Australian Bight, QM GH2379 GH4198). Victoria (Bass Strait, MV H756).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1972b). Victoria (Western Port MV F53818 Kott 1976).

The species has been taken at depths from 7 to 16m, often in caves where there is strong water movement.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are large, irregular, fleshy masses, with dark ridges along the surface and deep furrows between them. Furrows sometimes continue into cavities. These are pockets in the colony — a continuation of the outer surface which has become complex owing to its folding. Branchial apertures of zooids open all over the outer surface and into these pockets. Common cloacal apertures are large and conspicuous and several occur along the ridges. Common cloacal cavities are beneath the rather thin layers of zooid-bearing test in the furrows and ridges of the outer surface, and lining the pockets in the colony. The whole colony is traversed by spaces, either pockets in the test or common cloacal cavities.

Living colonies are pinkish beige with dark brown along the ridges which persists in the preserved material.

INTERNAL STRUCTURE: Zooids are only about 3mm long, with the abdomen only about half the length of the thorax. The branchial aperture is on a short siphon. The atrial siphon is long, projecting posteriorly from the posterior half of the dorsal border of the thorax to open into the cloacal cavities beneath the zooid-bearing layer of test. The rims of both the branchial and atrial apertures each have 6 lobes. Ten fine longitudinal muscles on the thorax extend along the abdomen and in a band along each side of the posterior abdominal stolon. A layer of fine transverse muscles surrounds the posterior two-thirds of the thorax. Circular muscles are around the branchial siphon and along the length of the atrial siphon. The branchial sac has 12 long elliptical stigmata in each of the 3 rows. The unperforated part of the pharyngeal wall anterior to the stigmata is long, occupying almost the whole anterior half of the pharynx. A shorter unperforated area is at the posterior end.

The gut forms a narrow tight loop, with the small, smooth stomach about halfway down the abdomen, and small posterior stomach also in the descending limb of the gut. The rectum extends from the pole of the gut loop and curves over into the proximal part of the atrial siphon. Gonads are present in the gut loop. They are mature in colonies collected in April from Western Port (Kott 1976), but not in those from Elliston Bay collected in May (Kott 1972b), nor the newly recorded ones from Ward I. collected in April (QM GH2378). The Victorian material has a large ovum attached to the side of the gut loop. Larvae are not known for this species.

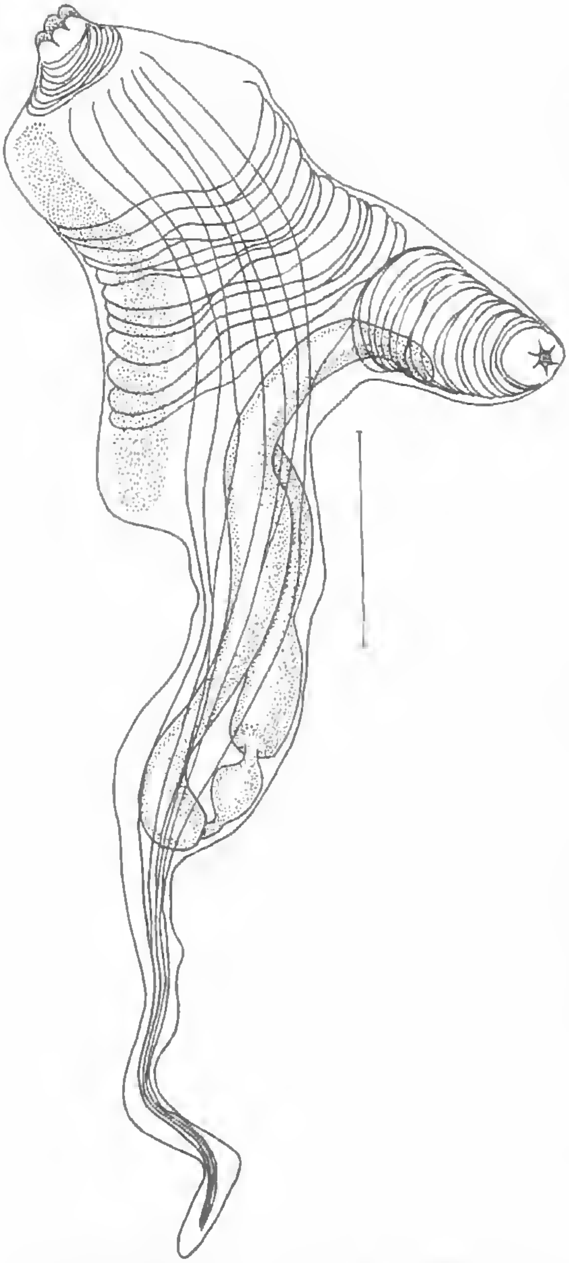


FIG. 38, *Hypodistoma mirabile* (QM GH2379): zooid. Scale: 0.5mm.

REMARKS: The species, with posteriorly directed atrial siphon opening into cloacal cavities beneath the zooid layers, resembles *H. deerratum* and *H. vastum* (from South Africa) although the zooids are smaller. *Hypodistoma vastum* has large embryos developing free in the test, although Millar (1963b) did not know how they got there. The large ovum attached to the abdominal loop in colonies of the present species from Western Port suggests that, instead of moving up the oviduct to develop in the brood pouch attached to the postero-dorsal corner of the thorax, the ova of this species are fertilised and initially incubated at the base of the oviduct. They could subsequently break away from the zooid to complete development in the test, as do the single embryos in the family Didemnidae and possibly in *Polydistoma* and certain *Distaplia*.

Genus **Distaplia** Della Valle, 1881
(nomen conservandum)

Type species: *Holozoa cylindrica* Lesson, 1830

The genus is characterised by its relatively short zooids each with a 6-lobed branchial aperture, and a wide atrial opening with the upper border produced into a large anterior lip. Zooids are arranged regularly in one or more circular, or oval, or long radiating, double row cloacal systems. Colonies are fleshy sheets, cushion-like or stalked. The test often has a spongy consistency. There always are 4 rows of long stigmata, usually crossed by a fine parastigmatic vessel. The stigmata in each row are progressively reduced in length toward the ventral line, leaving three small triangles of unperforated pharyngeal wall bounded by the ventral ends of rows of stigmata and the endostyle. Pointed dorsal languets are on the transverse vessels on the left of the dorsal sinus. The stomach wall is often folded. A posterior stomach is absent. Often (but not always) a large, spherical to oval gastric reservoir is in the gut loop. The junction between the mid-intestine and the rectum is always well defined and often has a distinct rectal valve. Gonads, consisting of a cluster of large testis follicles and a small group of ova, are either in the gut loop, or in a narrow-necked sac projecting from it. A conspicuous vascular process from the left side of the posterior end of the abdomen extends into the base or centre of the colony and down into the stalk (when one is present). Fine muscle bands extend obliquely from the branchial aperture and the intersiphonal space toward the postero-dorsal corner of the thorax. They may sometimes extend onto the abdomen but are inconspicuous and seldom detected. Muscle fibres have not been detected on the vascular process. Dorsal muscles in the intersiphonal region curve out around the anterior atrial lip and extend down each side of the aperture. Ova are fertilised, and embryos are brooded, in a loop of the distal part of the oviduct that projects into a sac from the postero-dorsal part of the thorax behind the atrial opening. The brood pouch becomes detached from the zooid to lie free in the test. Embryos probably are freed from the surface of the colony by rupture of the test.

Known larvae are all similar. They are large, with triradially arranged stalked, adhesive organs. The stalks of the adhesive organs develop large, rounded ampullary swellings at their base. They have a protruding axial cone of columnar cells surrounded by a cup-shaped structure consisting of an outer and parietal layer of specialised ectodermal cells. Each axial cone has a hyaline cap, the tip of which projects through an aperture in the larval test. Adhesive organs conform to those of *Distaplia occidentalis* Bancroft (see Cloney 1977). These are supported on a stolon from the posterior end of the oozooid which persists as a vascular appendage following metamorphosis. Usually both ocellus and otolith are in the cerebral vesicle. Adult organs, especially the branchial sac and the gut loop, are well developed and the former is especially large, occupying about one third of the larval trunk. Larvae are unusual in producing small buds from epicardial tissue at the junction of the oesophagus and pharynx (Berrill 1935b). The larval test contains crowded bladder cells and often pigment particles that obscure the developing organs. Most known species have only one embryo in each brood pouch — although a few species (*D. australiensis*, *D. muriella* n.sp. and *D. violetta* n.sp.) have more. Larvae are remarkably similar, with short tails, and large and sometimes almost cigar-shaped trunks containing vegetatively produced buds developed from the epicardial sacs at the posterior end of the pharynx.

The epicardial epithelium constitutes the regenerative tissue (Brien 1948) for replication in the adult. Replication occurs in 2 ways, *viz*. from numerous vegetative stolons (each containing a vestige of the left epicardial sac) isolated from the posterior end of the abdomen, near the vascular appendage; or from the remains of the anterior horns of the epicardial sacs that persist in the test following dissolution of the zooids (Berrill 1935b). Replication is prolific, but less so than in *Sycozoa*.

Species with several systems have randomly scattered cloacal apertures on the upper surface of sessile colonies and all around the zooid-bearing head of stalked colonies. *Distaplia systematica* Tokioka, 1959 from Japan has a single circular system in each separate lobe of the colony. In others with single systems, *viz*. *Distaplia australiensis* Brewin, 1953, *D. vallii* Herdman, 1886 and *D. smithi* Abbott and Trason, 1968 from California, zooids are arranged in rows along each side of the long canals that converge to a terminal cloacal aperture thus differing from *Sycozoa* which have long parallel canals that terminate around the flat, zooid-free upper surface.

Distaplia is remarkably homogenous and can confidently be regarded as monophyletic. Within the genus, species parameters are far from resolved. Differences in the colony — from cushion and extensive sheet-like forms fixed by a large area of the base, to stalked heads — have been regarded as intraspecific by many authors (Michaelsen 1930, Tokioka 1967a, Millar 1975). However, in most of the cases referred to by these authors, associated differences in the zooids have been detected that suggest genetic isolation and it is probable the colony form is a more reliable indicator of species identity than formerly thought.

In this study characters used to define a species are colony form (either sheet-like, sessile cushions or stalked), position of gonads (either in the gut loop or in a sac-like posterior abdomen), arrangement of the zooids (either around, or in double rows radiating from, the cloacal apertures; or a combination of both). There are also interspecific differences in the ratio of longitudinal thoracic muscles (from the branchial siphons) to oblique muscles (from the ventral mid-line), the shape of the stomach and its orientation, the condition of the stomach wall (either smooth, papillated, or folded, or with the internal lining raised into longitudinal ridges or reticulations), the number of testis follicles, and the number of embryos in the stalked brood pouch.

Remarkably little intraspecific variation occurs in the numbers of stigmata per row — rarely more than 4, and usually fewer, being involved. Further the characteristic number is present in all but the smallest vegetative zooids. There are one or 2 more present on one side of the branchial sac (usually the left) than the other, and usually 2 less in the posterior row than the anterior 3 rows. Previously reported intraspecific variations and ranges in the number of stigmata probably have resulted from difficulties in counting the stigmata of contracted thoraces. The major interspecific differences in the larvae are their size and the development of the ampullae around the base of the stalked adhesive organs.

The large, short-tailed larvae brooded for a long time in the parent colony, may not be widely dispersed. This could be the reason for the isolation that has resulted in the large numbers of apparently indigenous species of limited ranges known from tropical as well as temperate seas. In addition to the 12 indigenous Australian species reported on below, there are 4 indigenous Japanese species (Tokioka 1963), 3 indigenous South African species (Millar 1962), 3 indigenous New Zealand species (Brewin 1956b) and 2 species from the western Pacific (*D. vallii* Herdman, 1886 and *D. mikropnoa* Sluiter, 1909).

Tropical species are few (*D. cuscina* n.sp., *D. violetta* n.sp., *D. vallii* and *D. mikropnoa* from the Pacific; *D. stylifera* from the Indian Ocean). The last 3 have wide geographic ranges.

Key to the Species of *Distaplia* Recorded from Australia

1. Gonads in a sac posterior to abdomen 2
   Gonads not in a sac posterior to abdomen.. 6
2. Systems one per stalked head of colony.... ....*D. australiensis*
   Systems more than one per stalked head of colony 3
3. Stomach with external folds....4
   Stomach without external folds.... ....*D. prolifera* n.sp.
4. Testis follicles short, bunched 5
   Testes follicles long, parallel.... ....*D. violetta* n.sp.
5. Colonies usually stalked; parastigmatic vessels usually absent ....*D. stylifera*
   Colonies not stalked; parastigmatic vessels present....*D. tokioka* n.sp.
6. Stomach with external folds....7
   Stomach without external folds....8
7. Stigmata > 12 per row....*D. dubia*
   Stigmata not > 12 per row ....*D. pallida*
8. Colonies rope-like ....*D. retinaculata* n.sp.
   Colonies not rope-like....9
9. Systems with radiating double rows of zooids; oesophagus constricted distally ....*D. muriella* n.sp.
   Systems oval or circular: oesophagus not constricted distally 10
10. Stomach with conspicuous longitudinal ridges internally ....*D. cuscina* n.sp.
    Stomach without conspicuous longitudinal ridges internally 11
11. Thoracic muscles mostly longitudinal.... ....*D. regina* n.sp.
    Thoracic muscles not mostly longitudinal 12
12. Stigmata 22 or more per row....13
    Stigmata less than 22 per row ....*D. viridis*
13. Larval trunk > 2mm; thoracic muscles longitudinal and oblique.... ....*D. florida* n.sp.
    Larval trunk < 2mm; thoracic muscles mostly oblique ....*D. racemosa* n.sp.

Species recorded from adjacent areas, but not recorded from Australia are:

Distaplia capensis Michaelsen, 1934 from South Africa has similar colonies to *D. violetta* n.sp. but its gonads are in the abdomen. Its zooids, with stomach folds, resemble those of *D. pallida* (see also Millar 1962, 1964).

Distaplia durbanensis Millar, 1964 from South Africa is unique in having an abdominal brood pouch and a transverse atrial opening across the posterior third of the dorsal surface. It has a stalked colony and a rounded almost spherical head. Its stomach has internal papillations sometimes arranged in longitudinal lines as in *D. muriella* n.sp., and its gonads are in the gut loop.

Distaplia mikropnoa (Sluiter, 1909) from Indonesia, forms a massive colony that distinguishes it from the stalked *D. stylifera*. It also has an anastomosing network of stomach folds rather than the parallel ones of the latter species.

Distaplia skoogi Michaelsen, 1934 (see also Millar 1962) from South Africa, has small cushion-like colonies with circular systems. Its gonads are in a posterior abdominal sac. It lacks true stomach folds, but otherwise is similar to the South Australian *D. tokioka* n.sp. The cushion-like, broadly based specimens assigned by Millar (1975) to *D. stylifera* may be this species (see Millar 1975, fig. 17a) or *D. violetta* n.sp.

Distaplia stylifera: Millar, 1975 (part, specimen 21.3.1922 from Tocal) is not correctly assigned. The position of the rudimentary ovary projecting from the abdomen, is not an incipient posterior abdomen but is normal in juvenile vegetative zooids, as is the presence of an atrial siphon. Therefore, this specimen could belong to a species in which the gonads are contained

TABLE 5. Summary of Characters of the Species of *Distaplia* Recorded from Australia

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Posterior abdominal sac	Stigmata (per row)	Stomach	Larval trunk (length, mm)	Other
D. australiensis	A,te	Spencer Gulf–E. Tasmaina	stalked, head spherical–conical	present	11–13	16 folds	1.5	single system, lobe; long-necked brood pouch
D. stylifera	IWP,tr-te	Broome–Heron I.	″	″	12–18	16–20 folds	1.2	parastigmatic vessels often absent
D. prolifera n.sp.	A,tr	Port Hedland	stalked, head massive lobed	″	14–18	20 internal ridges	2.2	—
D. violetta n.sp.	WP,tr	Heron I.–Townsville	sessile–stalked	″	16–20	8–12 folds	1.6	lobed cloacal apertures
D. tokioka n.sp.	A,te	South Australia	sessile	″	12–16	12 folds	?	″
D. muriella n.sp.	A,te	Swan River	stalked, head spherical–conical	absent	12–16	smooth	1.5	valve at base of oesophagus; up to 6 embryos in brood pouch
D. florida n.sp.	A,te	South Australia–Byron Bay	sessile cushion–sheet	″	22–26	″	2.5	numerous larval ampullae; lobed cloacal apertures
D. regina n.sp.	A,tr	Heron I.	″	″	16–20	″	?	parastigmatic vessels absent; thoracic muscles longitudinal only
D. racemosa n.sp.	A,tr	Arafura Sea	″	″	24–26	″	1.8	test firm
D. cuscina n.sp.	WP,tr	Heron I.	″	″	16–22	16 internal ridges	1.5	—
D. dubia	WP,tr	Lord Howe I.	″	″	12–16	16 folds	?	—
D. pallida n.sp.	A,te	South Australia	″	″	8–12	12 folds	1.3	stomach folds flatten distally, systems irregular, crowded
D. viridis	A,te	SA–Heron I.	″	″	16–20	internal recticulations	1.5	vertical gut loop
D. retinaculata n.sp.	A,te	South Australia	rope-like	″	18–20	″	?	no thoracic brood pouch

[1] A, indigenous; WP, western Pacific; IWP, Indo-West Pacific; tr, tropical; te, temperate. [2] Range given anticlockwise around the continent.

in the gut loop. It resembles the new species *D. racemosa* n.sp. from northern Australia but is distinguished from it by the form of the colony — Millar's specimen consisting of separate lobes with a single system per head. It appears similar to *D. systematica* Tokioka, 1958 from Sirahama (Japan), Millar's drawing (Millar 1975, fig. 18) showing the preponderance of transverse muscles characteristic of the Japanese species. *Distaplia vallii* Herdman from the Philippines has colonies consisting of similar stalked heads, but it has double row systems.

Distaplia tahihuero Monniot and Monniot, 1987 from Tahiti has colonies closely resembling those of *D. cuscina* n.sp. both in form and in colour — both living and in preservative. Zooids differ only in the fewer testis follicles — 6 to 8 in *D. cuscina* and 3 or 4 in the specimen from Tahiti. This may indicate no more than a population difference.

Distaplia vallii Herdman, 1886 from the Philippines (not *Holozoa vallii*: Van Name, 1918 < *D. cuscina* n.sp.) has numerous stalked heads from a common base, each head a single system with double rows of zooids converging to the terminal cloacal aperture. The colonies most resemble those of *D. australiensis*, but the gonads of the Philippine specimen are in the gut loop rather than in a posterior abdominal sac.

Distaplia australiensis Brewin, 1953

(Fig. 39. Plate 9a)

Distaplia australiensis Brewin, 1953, p.61. Kott 1957a, p.95; 1975, p.1.

DISTRIBUTION

NEW RECORDS: South Australia (Spencer Gulf, QM GH2288; St Vincent Gulf, QM G10126). Tasmania (d'Entrecasteaux Channel, TM D251 D2021; Huon Channel, TM D1850). Victoria (Bass Strait, QM G11871). Queensland (Calliope River, QM GH2158).

PREVIOUSLY RECORDED: South Australia (Spencer Gulf — SAM E1993, QM G9259 Kott 1975). Tasmania (S. Tasmania — AM U384 Brewin 1953, Kott 1957a; d'Entrecasteaux Channel – Kott 1957a).

The maximum depth at which the species has been taken is 50m. Most records of this species are from a relatively small area between Spencer Gulf and the eastern coast of Tasmania. The record from Gladstone is anomalous. It either represents an isolated population of this species, or it indicates inadequate sampling of a species with a continuous range between tropical and temperate waters.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of a number (up to 10) of spherical to conical heads, up to 1.5cm in diameter, on fleshy cylindrical stalks longer than the head and about half its diameter. Stalks are joined to one another basally and to a mat of test. Zooids are arranged in double rows radiating from a large terminal cloacal aperture in the centre of the upper surface of the head. Intervals between the double rows of zooids are where the cloacal canals extend beneath the surface test from the terminal cloacal cavity down the sides of the colony. The sides of the zooids away from the canals are close to the zooids in the adjacent row. The test has a spongy consistency.

Living colonies are blue-grey. In recently preserved material colonies are greenish-blue, the test containing inky-blue particles that colour the preservative. Later this colour is lost and the colonies are beige.

INTERNAL STRUCTURE: Zooids are small, the thorax and abdomen together being about 4mm long, and the sac-like posterior abdomen attached to the right side of the posterior end of the abdomen is, when the gonads it contains are mature, only about half that length. About 30 fine muscle bands are on the thorax, about half extending obliquely from the endostyle toward the posterior end of the pharynx. Muscles were not detected on the abdomen. The dorsal muscles cross the mid-dorsal line around the top of the atrial opening where they curve out into the pointed lip that is produced from the upper border of the opening. They then pass down along each side of the opening. These muscles are crossed by strong bands from the branchial aperture extending along the centre of the atrial lip; and a few extend from the borders of the atrial aperture transversely across the sides of the body. The atrial opening is asymmetrical, one side of the aperture exposing more of the branchial sac than the other. The asymmetry is dependent on the side of the cloacal canal on which the zooid is located, the side facing the cloacal canal being the one on which the branchial sac is exposed. There are 13 stigmata per row in the 3 anterior rows and 12 in the posterior rows on the left, and 12 and 11 respectively on the right. A fine parastigmatic vessel crosses each row of stigmata.

The stomach, about halfway down the abdomen, is short on its right side where the oesophageal opening is located, while the left side is long and widely curved. The oesophagus bends ventrally to open into the stomach. The stomach wall has about 16 narrow ridges in its internal wall that appear as shallow folds on the surface. They extend from around the oesophageal opening to the pyloric end. The mid-intestine opens into the rectum near the posterior end of the descending

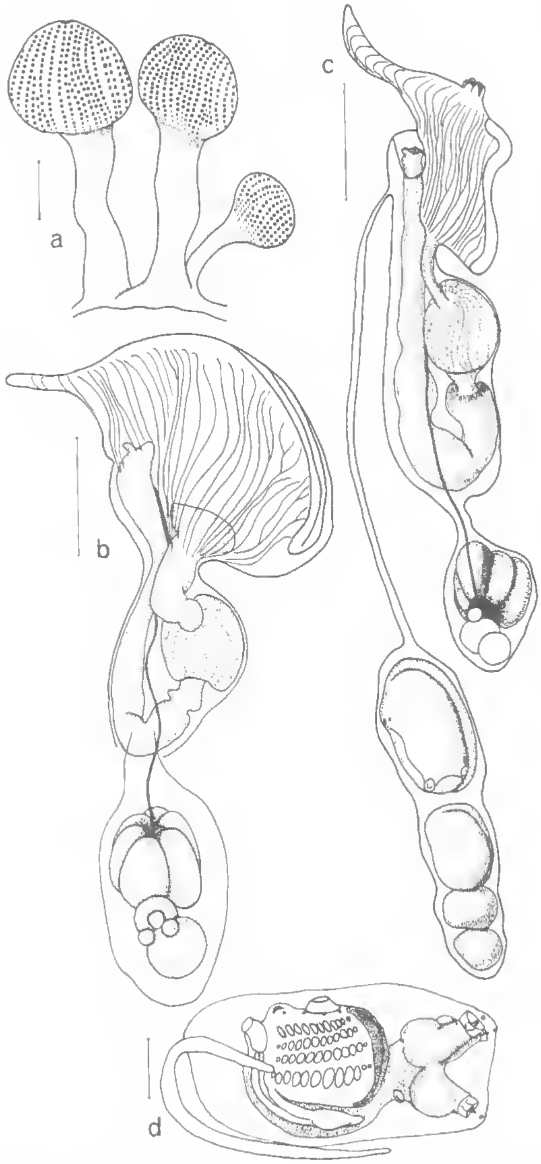


FIG. 39. *Distaplia australiensis*: **a**, colony (QM GH2288); **b,c**, zooids (QM G9259 GH2158); **d**, larva (QM GH2158). Scales: **a**, 5mm; **b**, 0.5mm; **c**, 1mm; **d** 0.25mm.

limb of the gut loop. There is a conspicuous gastro-intestinal reservoir suspended about halfway along the duct between the stomach and the proximal part of the intestine. The specimens from Queensland have about 24 stomach folds.

Gonads are contained in the posterior abdominal sac connected to the right side of the posterior end of the abdomen by a narrow neck. The testis consists of a barrel-shaped mass of 5 to 6 long follicles joined to the vas deferens at the anterior end. A clump of about 5 ova of various sizes are at the posterior end of the testis. Brewin (1953) recorded specimens collected in September with a single early embryo developing in the brood pouch attached by a long narrow neck to the postero-dorsal part of the thorax just behind the atrial opening. Specimens collected in April (QM G11871), July (TM D1850) and September (QM G10128) had no embryos. Previously recorded specimens from Spencer Gulf collected in September (Kott 1975) have a single early embryo in each brood pouch, but no tailed larvae. Specimens taken in May from Spencer Gulf (QM GH3288) had up to 3 developing embryos, one at an advanced stage, in the brood pouch. Specimens from the Calliope River collected in October have the characteristic long-necked brood pouches and each contains 3 to 5 developing embryos. The evidence suggests breeding periods in spring and autumn.

The larva has a long trunk (1.5mm) but the tail reaches only halfway along it. There is an ocellus and otolith. The stout stalks of the adhesive organs expand basally.

REMARKS: Re-examination of specimens from Upper Spencer Gulf and d'Entrecasteaux Channel (Brewin 1953 and Kott 1957a, 1975) revealed the numbers of stigmata in each row are as reported above. Further, the numbers of thoracic muscles and stomach folds reported by Kott (1975) for the South Australian material are too low, the actual numbers being in the vicinity of 30 and 16 respectively. The parastigmatic vessels, which were overlooked by Brewin (1953), are always present.

Distaplia australiensis is distinguished from all other Australian species by its long, double rows of zooids radiating from a single, terminal cloacal opening comprising a single system in each stalked head. Like *D. smithi* Abbott and Trason, 1968 from California, it has a number of stalked heads joined basally to common test. The Australian species has a longitudinally folded stomach in contrast with the areolated stomach surface in the California species.

Distaplia vallii Herdman, 1886, from the Philippines, also has stalked heads arising from a common base, each head consisting of a single system, with double rows of zooids radiating from a terminal common cloaca. It is distinguished from *D. australiensis* principally by the absence of a posterior abdomen. The Atlantic species *Distaplia bursata* (Van Name, 1921), which Michaelsen (1930) thought to be a synonym of *D. stylifera*, has a colony and other characters more closely resembling the present species, although it has shorter stalks and flatter heads.

The specimen from the Calliope River, Gladstone differs from those from southern Australian locations in the greater number of folds on the stomach. On information available the separation of the Gladstone population from the southern Australian ones is not justified although the record from such a widely separated location is surprising.

Distaplia cuscina n.sp.

(Fig. 40)

Holozoa vallii: Van Name, 1918, p. 140.
Distaplia vallii: Millar, 1975, p. 227. Kott, 1981, p. 149.

DISTRIBUTION

TYPE LOCALITY: Queensland (Capricorn Group, Wistari Reef, rubble fauna, low tide, coll. P. Kott 17.6.85, holotype QM GH4381, paratypes QM GH4124).

FURTHER RECORDS: Queensland (Capricorn Group, QM GH4120–3 GH4125–6 GH4200).

PREVIOUSLY RECORDED: Philippines (Van Name 1918, Millar 1975). Fiji (Kott 1981).

Fijian and Australian records are from intertidal locations. Records from the Philippines are from depths to 40m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are soft cushions not more than 5mm thick. Zooids, opening onto the upper surface of the colony, are arranged in circular systems around central cloacal apertures. Borders of the cloacal apertures do not protrude from the surface of the colony.

The test is soft in smaller colonies, but spongy in larger ones. Living colonies are cloudy rose, soft lilac, having a mixture of dark purple, lavender and white pigment cells in the test. Zooids are white. Freshly preserved colonies, with indigo pigments cells in the test, are slate-blue; subsequently they become light green fading to beige.

INTERNAL STRUCTURE: Zooids are small, usually less than 2mm long, excluding the relatively short, fine vascular appendage. About 20 fine thoracic muscles extend from the endostyle and branchial siphon toward the postero-dorsal corner of the body. Dorsal muscles curve out into the very long atrial tongue before extending posteriorly along each side of the atrial aperture. Also longitudinal muscles in the atrial tongue cross these dorsal muscles. The tip of the atrial tongue has 3 short lobes that insert into the test around the cloacal aperture. Branchial lobes are only shallow. The usual 4 rows of stigmata are crossed by a fine, often inconspicuous parastigmatic vessel. Some slight variation occurs in the number of stigmata, *e.g.* 20 to 22 in the three anterior rows on the left, and 18 to 20 in the posterior row. On the right there are 18 to 20 in the anterior rows, and 16 to 18 in the posterior row.

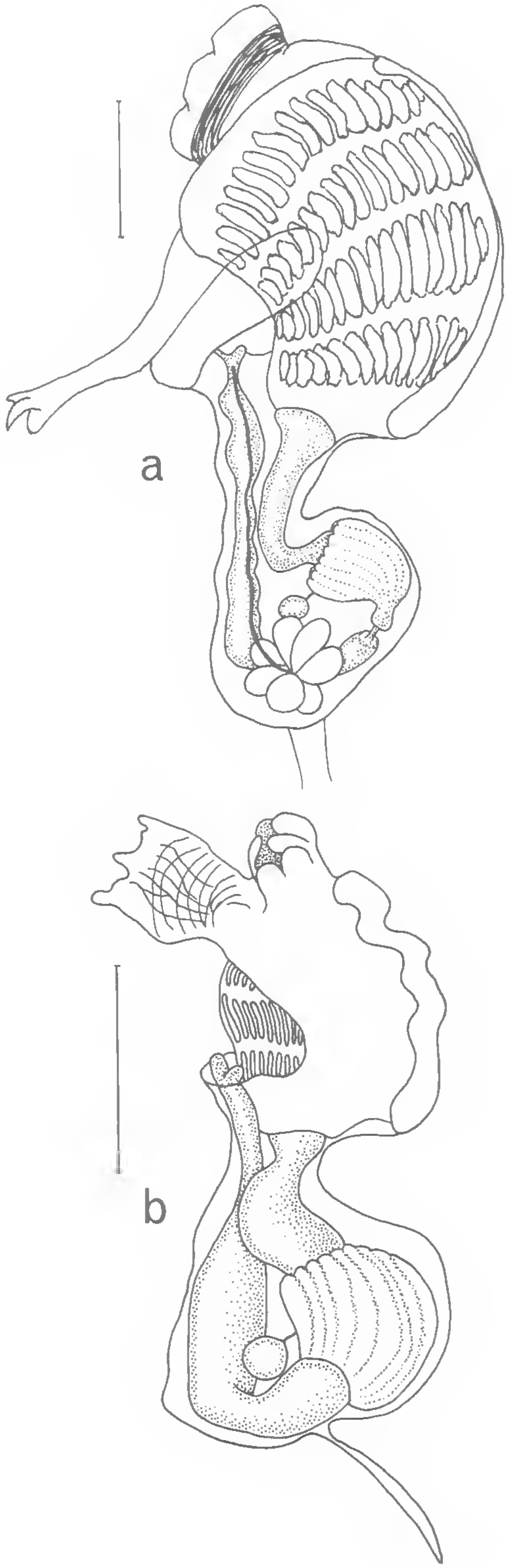
The gut loop is vertical, the oesophagus relatively long and the more or less elliptical stomach, with about 16 fine internal striations or ridges in its glandular wall, is in the posterior third of the abdomen. A distinct rectal valve separates the rectum from the mid-intestine. A conspicuous gastric reservoir is in the gut loop. Mature zooids have a tight circle of 6 to 8 pear-shaped follicles on the right side of the pole of the gut loop. They converge to the centre of the circle where they join the proximal end of the vas deferens. There is often a small ovum (just posterior to the proximal end of the vas deferens), and frequently it projects from the side of the abdomen.

Specimens collected from the Capricorn Group in March (QM GH4122) and May (QM GH4200) have a single embryo in each brood pouch (attached to the postero-dorsal corner of the thorax).

Larvae have a trunk about 1.5mm long, with the tail wound three-quarters of the way around it. Each of 3 tri-radially arranged adhesive organs with stout stalks has a pair of ectodermal ampullae near its base. An ocellus and an otolith are in the cerebral vesicle. The larval test contains pigment particles and looks frothy owing to the packed bladder cells. This makes it difficult to see the larval organs.

REMARKS. The soft pink-lilac of this species is similar to that of *Distaplia violetta* n.sp. and the two species are readily confused in the field. However, in the latter species both branchial and cloacal apertures are much more conspicuous, the colony is thicker and often stalked rather than sessile, and it has purple and some brownish or yellow pigment particles in the test while the present species has purple and lavendar pigment only. Zooids of *D. violetta* are readily distinguished, being larger, with conspicuous, relatively broad external stomach folds and a posterior abdomen containing the gonads.

The type specimen of *Distaplia vallii* Herdman, 1886 is from the Philippines. It consists of many stalked heads arising from a common basal stolon, each head consisting of a single system with double rows of zooids converging to a single terminal common cloacal aperture. The colony resembles that of *D. australiensis* and is different from the colonies of the present species with their several circular systems that formerly were assigned to *D. vallii* by Van Name (1918), Millar (1975) and Kott (1981). The zooids of Herdman's species are distinguished also by their primarily oblique and



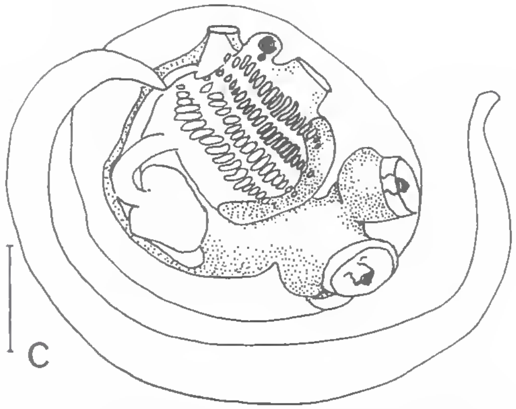


FIG. 40, *Distaplia cuscina* n.sp.: **a,b**, zooids (holotype QM GH4381 GH4123); **c**, larva (QM GH4122). Scales: **a,b**, 0.5mm; **c**, 0.25mm.

transverse muscles. The other specimen Herdman assigned to *D. vallii* is from the Mediterranean and it appears to be distinct from any of the Pacific Ocean species (see Van Name 1918).

Distaplia tahihuero Monniot and Monniot, 1987 from Tahiti closely resembles the present species both in colour and colony form. The zooids of both species are of similar size, have the same number of stigmata per row, and the same internally ridged stomach. The ovum projects from the side of the abdomen in the same way as it often does in this and other species of *Distaplia*. There are fewer (3 or 4) testis follicles in *D. tahiheuro* and the larva is smaller than that of the present species.

Kott (1981) suggested the synonymy of *Distaplia dubia* (Oka, 1927c) with the present species. However, *D. dubia* has a stomach with external folds that more closely resembles that of *D. stylifera* than the present species.

Distaplia dubia (Oka, 1927)
(Fig. 41a. Plate 9b)

Leptobotrylloides dubium Oka, 1927c, p. 607.
Distaplia dubia: Tokioka, 1953, p. 206; 1954c, p. 82; 1967c, p. 240.
Not *Distaplia* aff. *dubia*: Tokioka, 1967c, p. 240.
Distaplia japonica Tokioka, 1951b, p. 169.

DISTRIBUTION

NEW RECORDS: New South Wales (Lord Howe I., QM GH52).

PREVIOUSLY RECORDED: Japan (Japan Sea, Seto Naiki Sea, Sagami Bay — Oka 1927c, Tokioka 1951b, 1953, 1954b, 1967c).

DESCRIPTION

EXTERNAL APPEARANCE: The colony forms a fleshy encrusting sheet. The test has a soft, spongy

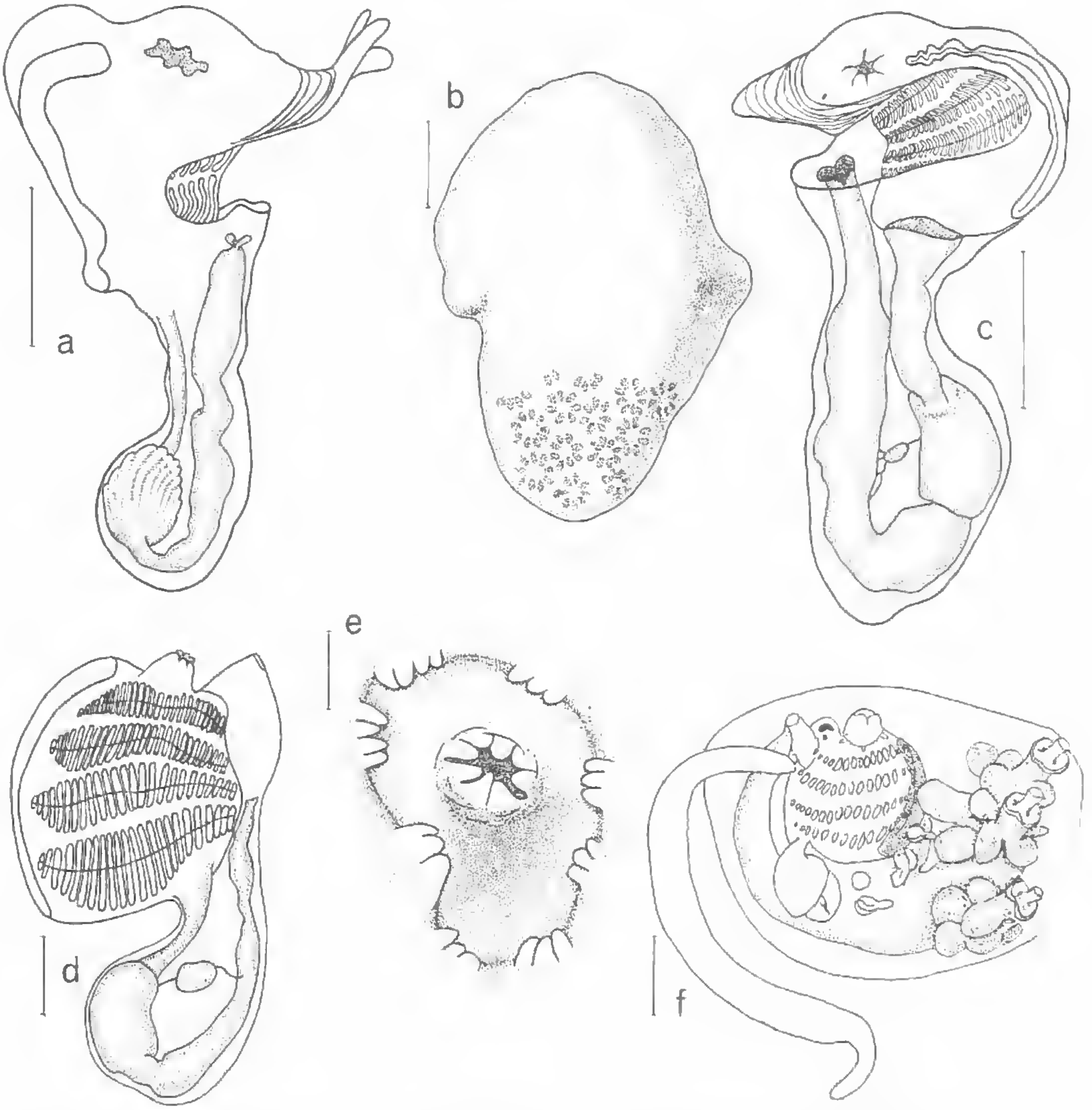


FIG. 41. *Distaplia dubia*: a, zooid (QM GH52). *Distaplia florida* n.sp.: b, colony (QM GH4164); c, zooid (holotype QM GH4103); d, juvenile vegetative zooid (SAM E2039); e, branchial apertures, obscured by their enlarged ventral lobes, surround a lobed common cloacal opening (MV F53292); f, larva (holotype QM GH4103). Scales, a,e,f, 0.5mm; b, 1cm; c, 1mm; d, 0.25mm.

consistency. Zooids are in circular systems. In life the present specimen was blue-grey with orange patches. When first preserved it contained dark pigment cells in the surface, especially in the vicinity of the zooids. However, long-term preservation has left it a dirty beige colour.

INTERNAL STRUCTURE. The branchial aperture has 6 shallow lobes. Three tongue-like projections occur on the tip of the long atrial lip. The usual fine longitudinal thoracic muscles occur and dorsal muscles curve out into the atrial tongue. The thorax is about twice the length of the abdomen.

In the branchial sac 16 stigmata are in the 3 anterior rows on the left and 14 in the posterior row. On the right 14 stigmata are in the anterior rows and 12 in the posterior row. Parastigmatic vessels were not detected, but it is possible they have been lost or are obscured in these contracted specimens. The oesophagus is fairly long and curves horizontally to enter the obliquely oriented stomach, which is shorter along its mesial side than along its outer curved surface. The stomach has 16 fine longitudinal folds. Gonads were not detected in this specimen. It is probable they develop in the gut loop, as a posterior abdominal sac is not present and there would not be space for one in these relatively thin sheet-like colonies.

REMARKS: Although Lord Howe I. is geographically isolated from the Japanese location from which this species has been recorded previously, the specimen is indistinguishable from the Japanese material. Tokioka (1953) described specimens from Japan as greyish-brown, or shades of pink, or dirty greyish-orange and the newly recorded specimen is patterned in grey and orange. The Japanese specimens have 15 to 20 stigmata per row, 16 fine stomach folds can be observed on the outer wall of the stomach, and the test is the same consistency as the present species.

Amongst other species of this genus, its colony most resembles *D. cuscina* n.sp. However, the latter species has more stigmata per row, and although its stomach has longitudinal ridges internally, externally it is smooth. *Distaplia viridis* from South Australia has similar systems, but is distinguished by its more numerous stigmata and smooth stomach. *Distaplia pallida* n.sp. does have a folded stomach, but the folds are wider than those in the present species and it has more complex cloacal systems and fewer stigmata.

If this Lord Howe I. specimen is correctly assigned a much wider range is predicted for this species.

Distaplia florida n.sp.

(Fig. 41b–f. Plate 9c,d)

DISTRIBUTION

TYPE LOCALITY: New South Wales (Julian Rocks Bryon Bay, reef, 10m, coll. N. Coleman 30.3.75, holotype QM GH4103).

FURTHER RECORDS: South Australia (Great Australian Bight SAM E1999 E2039, QM GH4180 GH4184). Tasmania (King I, MV F53292).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies form soft, flat cushions about 4cm in diameter and slightly less than 1cm thick. Zooids are in circular systems — in groups of about 8 around each cloacal cavity with its central cloacal opening. Cloacal apertures are conspicuous, each on a protruding siphon that rises from the centre of a depressed area. The border of the aperture is divided into lobes into which the atrial lips of the zooids are inserted. Branchial apertures open around the outer walls of the surface depressions. In the preserved specimens, ventral lobes of each branchial aperture are long and the openings are directed in toward the cloacal aperture. Systems are evenly spaced, with a small area of zooid free test between them. The test has a spongy consistency. The surface test over each system is extremely thin, and possibly the surface depressions, over the zooids and cloacal cavity, are inflated and raised in life. Free larvae in the holotype colony beneath the surface outside the circles of zooids are probably about to be liberated.

In preservative colonies are grey, beige, or pinkish-cyclamen, cloudy throughout and with red pigment particles and clouds of white granules in the surface. In life the holotype colony was purple and pink (*fide* N. Coleman). Colonies from South Australia were orange or dark red with distinct black circles around cloacal apertures (*fide* S. Shepherd QM GH4164) or very pale pink or cream (SAM E1999).

INTERNAL STRUCTURE: Zooids are about 4mm long, the thorax and abdomen about equal length when the thorax is relaxed. The branchial aperture has 6 lobes. The atrial aperture is wide, with a pronounced anterior lip and some asymmetry of the opening, depending on the zooid's orientation to the cloacal cavity.

Numerous fine longitudinal and oblique muscle bands occur, the most dorsal curving out into the atrial lip which is sometimes long and pointed. The branchial opening is 6-lobed. On the left are 24 and 26 long, rectangular stigmata in the posterior and each of the 3 anterior rows, respectively. On the right are 24 stigmata in the anterior 3 rows and 22 in the posterior row. Each row is crossed by a parastigmatic vessel.

The abdomen is narrow, the gut forming a vertical loop. The smooth, kidney-shaped, yellowish stomach lies vertically in the posterior half of the abdomen. The oesophagus is rather long and narrow. A short, broad duodenal area is separated from the rectum by a slight constriction in the posterior end of the descending limb of the gut loop. Gonads are in the gut loop, although neither sex is mature in the type specimen. In the buds scattered randomly in the test between the adult zooids are well-developed testes consisting of a circle of about 12 club-shaped follicles converging into the proximal end of the vas deferens in the centre of the circle.

Larvae, one in each brood pouch, are large, the trunk being 2.5mm long. The tail is about the same length as the trunk and, when curved around it, barely reaches the anterior end. In the mature larva the oozooid occupies the posterior end of the trunk. It has a full complement of stigmata with a parastigmatic vessel crossing each row. There is an ocellus and an otolith in the cerebral vesicle. Five small buds move progressively from the oesophageal region of the oozooid, ventrally and then dorsally around the left side of the middle of the trunk — *i.e.* around the base of the adhesive apparatus that occupies the anterior half of the trunk. The adhesive apparatus consists of 3 large, anterior stalked adhesive organs, 2 dorsal and one ventral, each consisting of a central cone of columnar cells rising from the base of a relatively shallow epidermal concavity. The base of each of the stalks of the adhesive organs is expanded into about 7 balloon-like elongated ectodermal ampullae.

REMARKS: The species resembles the South Australian *D. viridis*, having similar circular systems, zooids with similar body musculature, a vertical gut loop with a smooth yellowish, kidney shaped stomach, and gonads in the loop of the gut. The present species is distinguished by having larger zooids with more stigmata in each row, a cushion- rather than sheet-like colony and a much larger larval trunk with more elaborate adhesive apparatus, and it lacks the dark pigmentation of *D. viridis*. *Distaplia pallida* n.sp. is distinguished by its sheet-like colony, its folded and horizontally oriented stomach, fewer stigmata, more transparent test and small zooids.

The colonies of *D. florida* resemble those of *D. tokioka* n.sp., as do the circular systems. However the latter species has its gonads in a sac posterior to the abdomen, while those of the present species are in the gut loop.

Distaplia muriella n.sp.
(Fig. 42)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Blackwall Reach, Swan River estuary, 20m muddy bottom, coll. 2.4.60, holotype WAM 135.75; Swan River estuary, Rocky Bay, at edge of channel, coll. WA Naturalists November 9, paratypes WAM 32.75).

FURTHER RECORDS: Western Australia (Swan River, WAM 1003.83 17.87; Garden Island).

Apart from a single specimen recorded from Garden Island, just outside the Swan River estuary, the records of the species are from within the estuary — where apparently it is indigenous. The Swan River estuary in the vicinity of the type locality — Blackwall Reach — has a deep pocket of salt water that persists through the winter beneath the fresh water inundations that occur at that time (Spencer 1956). At Rocky Bay, which is on the opposite shore from Blackwall Reach, specimens have been taken from intertidal and shallow water in the summer when the salinity is marine.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are irregular. Some small mushroom-shaped, flat-topped, zooid-bearing heads are supported on upright and recumbent stalk-like outgrowths of common basal test. Some are attached to a large worm tube by a thin basal membrane (WAM 135.75). Also large areas of the basal test thicken to 0.5cm beneath irregularly shaped flat-topped zooid-bearing lobes, 5cm in maximum extent. These lobes slightly overlap the thickened basal test, and sometimes one another, around their periphery.

Zooids usually are in double rows radiating from 2 or 3 common cloacal openings in the centre of the flat upper surface of the smaller mushroom-like heads. In larger plate-like lobes the number of common cloacal apertures increases and they become more dispersed over the upper surface. Zooids sometimes are arranged in a circle around a cloacal aperture although as zooids are added to the system, the double rows develop and radiate out from the aperture. The test is soft and semi-transparent. In preservative colonies are pastel pink and blue, both colours occurring in the one colony and sometimes in the one lobe. Some specimens from Blackwall Beach are muddy grey in preservative, owing to the mud content in the gut of the zooids. The pigment is in particles in the surface test.

INTERNAL STRUCTURE: The small branchial aperture is terminal and is not lobed. The atrial aperture is a wide opening with the upper border produced into a long pointed lip. About 30 fine muscle bands are on the thorax. Dorsal ones extend across the dorsal line between the atrial and branchial apertures, curving out into the atrial lip; others radiate from the branchial aperture; and the ventral ones extend from the endostyle toward the postero-dorsal corner of the thorax. Muscles are present, but are most inconspicuous on the abdomen. There are 16 and 14 long rectangular stigmata in anterior rows on left and right respectively, and 14 and 12 in the posterior rows. Fine parastigmatic vessels are present.

The long, elliptical, vertically oriented and rigid stomach is yellow. It is smooth externally but internally it is papillated. Occasionally the papillations seem in longitudinal lines appearing as fine longitudinal striations. The oesophagus is constricted before it enters the stomach.

Gonads are in the gut loop and consist of a rosette of up to 12 testis follicles with a large central ovum and up to 2 smaller ones on the right side of the gut loop. A long brood pouch is attached by a long, narrow neck to the postero-dorsal corner of the thorax to the right of the rectum. The brood pouch, containing up to six embryos, extends toward the base of the colony without curving, although its distal tip is bent upwards.

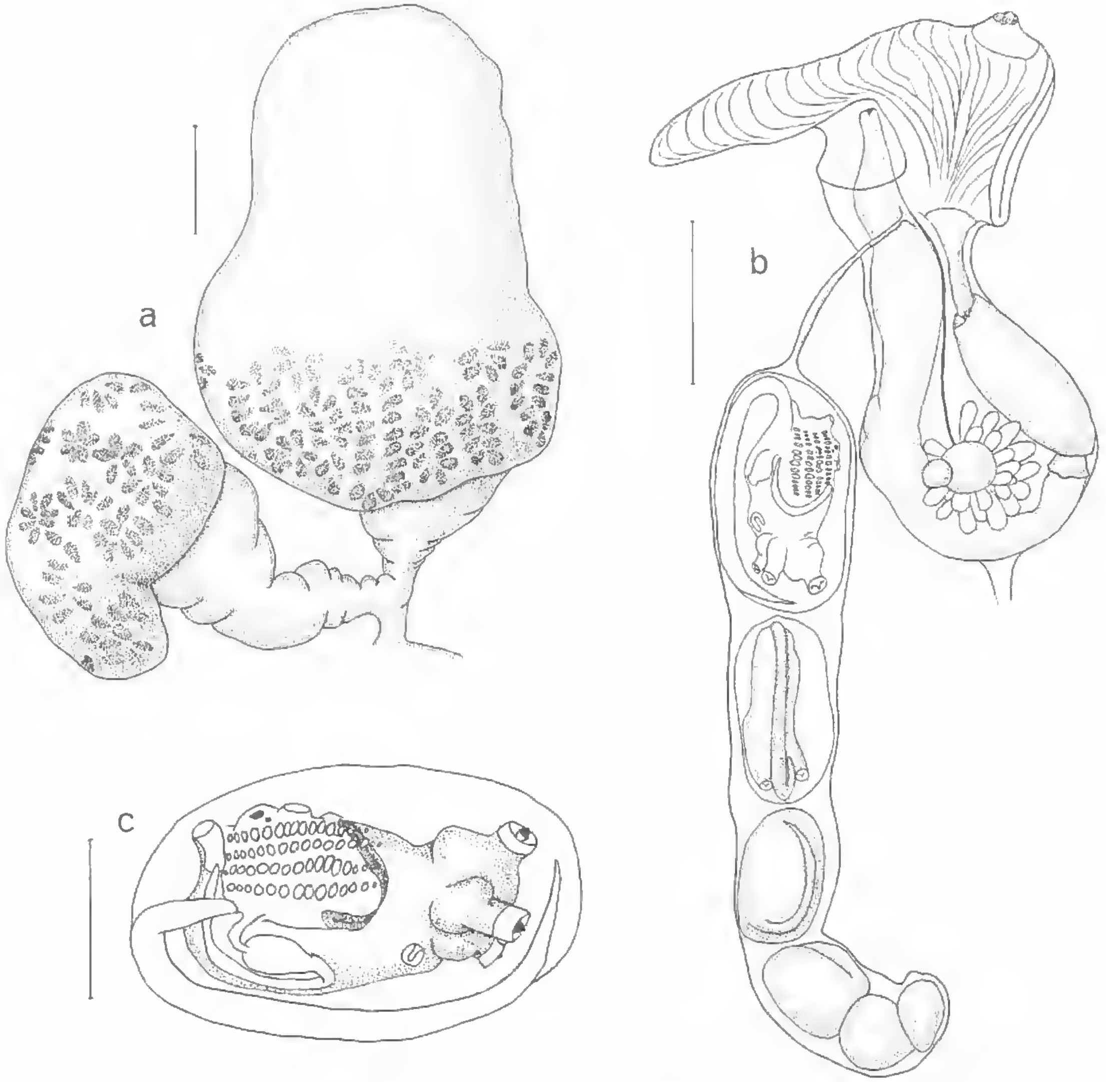


FIG. 42, *Distaplia muriella* n.sp. (holotype WAM 135.75): **a**, colony; **b**, zooid; **c**, larva. Scales: **a**, 5mm; **b**, 1mm; **c**, 0.5mm.

Developing embryos and tailed larvae are present in the holotype and paratypes from the Swan River taken in November.

Larvae are large, with a long (1.5mm) almost cylindrical trunk and a tail only slightly longer. There is an otolith and an ocellus in the cerebral vesicle.

REMARKS: Colonies resemble most closely those of *D. australiensis*, with double row systems radiating from cloacal apertures and extending down the sides of the colony. However, zooids differ, those of the present species having their gonads in the loop of the gut rather than in a posterior abdominal sac. Zooids of the tropical species *D. cuscina* n.sp. are similar to those of the present species, the stomach having the same elliptical shape and vertical orientation, although in *D. cuscina* the systems are more consistently circular, the number of stigmata in each row is greater, the stomach has internal ridges, and the oesophagus is not constricted before it enters the stomach.

Other known species with a smooth stomach and gonads enclosed in the abdomen, *viz. D. regina* n.sp., *D. florida* n.sp. and *D. racemosa* n.sp., have circular rather than double row systems converging to terminal cloacal apertures, and their colonies are cushion-shaped rather than stalked.

The constriction at the distal end of the oesophagus just before it enters the stomach is an unique feature in *D. muriella* helping to distinguish it from all other species. The numerous (6) embryos in the brood pouch are an unusual feature of the present species which it shares with *D. australiensis* (which has from one to 5). *Distaplia violetta* n.sp. sometimes has 3 but other species have no more than one.

Colonies of this species from the Swan River estuary in both April and November are in an active state — sexual reproduction as well as vegetative replication occurring in the same colony at these times.

Distaplia pallida n.sp.

(Fig. 43. Plate 9e)

Distaplia viridis: Kott, 1972a, p. 7 (part, fig. 6 specimens from Hallett Cove).

DISTRIBUTION

TYPE LOCALITY. Victoria (Portsea, on jetty pile, 4m, coll. N. Coleman 13.3.75, holotype QM GH4102; 2m, coll. G. Russ 16.3.78, paratype QM G11923).

FURTHER RECORDS. South Australia (St Vincent Gulf – SAM E1998 Kott 1972a; Great Australian Bight — QM GH 4189). Victoria (Portsea, QM G11924). Tasmania (Tinderbox, QM G9994).

DESCRIPTION

EXTERNAL APPEARANCE: The sheet-like colonies are thin (not more than 0.5cm thick) and sometimes extensive, growing around rubble. In preservative the test is gelatinous and almost transparent, and the zooids show through it as white dots. Zooids are in circular to oval systems of up to 15 zooids. Each system has a cloacal aperture at its centre or toward one end. Sometimes one end of an oval system is extended into a short, double row. The living specimens

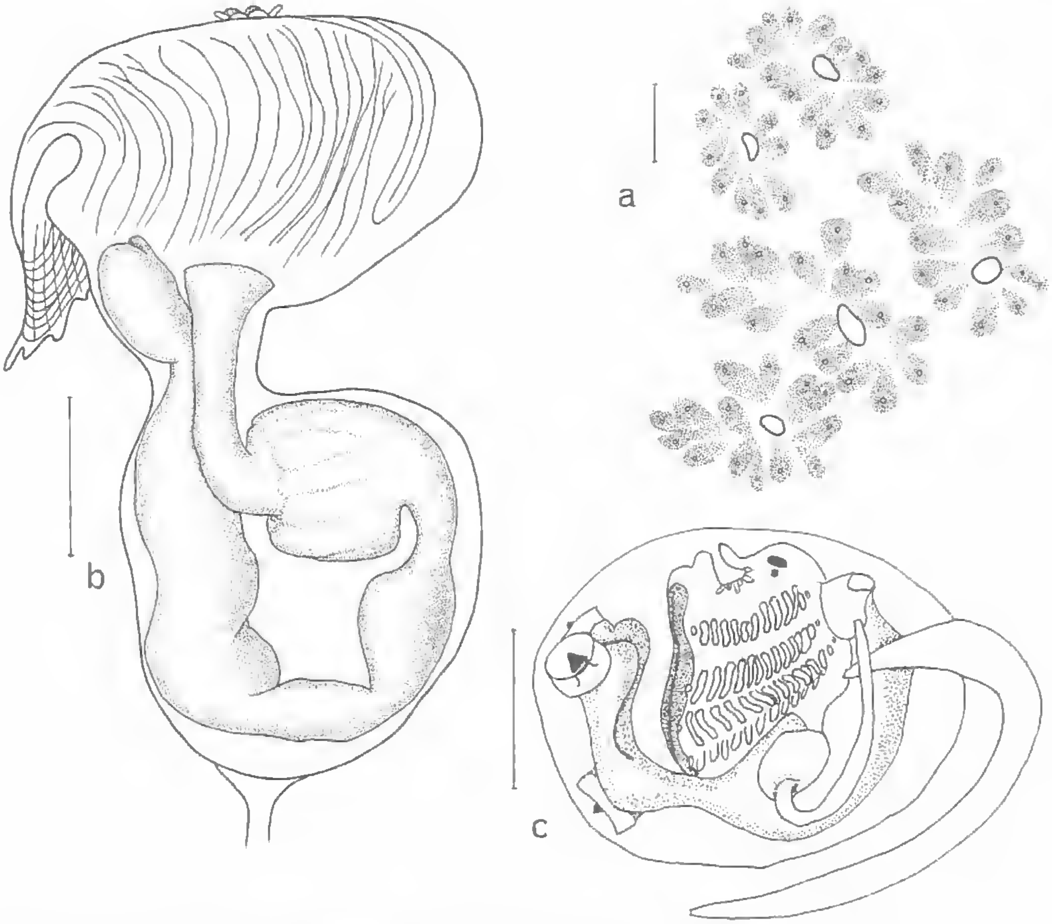


FIG. 43, *Distaplia pallida* n.sp.: **a**, arrangement of zooids in system (paratype QM G11923); **b**, zooid (paratype QM G11923); **c**, larva (SAM L1998). Scales: **a**, 2mm; **b**,**c**, 0.5mm.

are a pale to bright yellow and orange (QM GH4189), or the zooids are orange in a transparent test (SAM E1998).

Internal Structure. Zooids with a contracted thorax are up to 3mm long, but usually are smaller. About 20 fine longitudinal and oblique muscles are present on the thorax. There are 6 small branchial lobes. The atrial aperture is the usual wide asymmetrical opening. It has a long anterior lip with 3 or 4 pointed or rounded tooth-like projections along its flat-ended outer tip, which is often oblique and asymmetrical rather than straight, corresponding to the asymmetry of the opening itself. Muscles extend from the branchial aperture along the centre of the atrial lip, crossing the dorsal muscles that curve out into the lip.

On the left are 10 and 12 stigmata in the posterior and each of the three anterior rows of stigmata respectively, and on the right the numbers are 10 in the anterior rows and 8 in the posterior row. Each row is crossed by a parastigmatic vessel.

About halfway down, the oesophagus makes an abrupt, right angled bend toward the ventral surface to enter the stomach, which is short and almost barrel-shaped and lies at right angles to the longitudinal axis of the zooid. The stomach has about 12 deep, rounded folds at its cardiac end. These fade out at the pyloric end, where the stomach narrows. The duodenal region of the gut turns posteriorly, at right angles to the long axis of the stomach. The mid-intestine occupies the distal part of the descending limb of the gut loop before narrowing slightly to open into the rectum where, in some specimens with an empty gut, a rectal valve can be seen. Thus the gut loop frames an almost rectangular area in the lower half of the abdomen. Gonads are in the gut loop and consist of a circle of male follicles and a single egg.

Gonads are mature in specimens collected from South Australia in December (SAM E1998), but not in any of the colonies collected in March or April. There are vegetative buds in the test amongst the adult zooids, but no gonads were observed in these small vegetative individuals.

One tailed larva is present in each brood pouch in colonies collected from St Vincent Gulf in December (SAM E1998). The trunk is almost spherical, 1.35mm long with a short tail extending only about one-third of the way around the circumference of the trunk. The 3 triradially arranged, almost sessile adhesive organs are on a frontal plate. Four rows of stigmata are present, together with ocellus, otolith and a well developed gut loop.

Remarks. In preservative, these investing colonies can be mistaken for the sympatric *D. viridis* or *D. tokioka* n.sp. *Distaplia pallida* is distinguished from *D. viridis* by its smaller zooids with fewer stigmata, larger and more variable systems, the right-angled bend in the oesophagus, deeply folded stomach, more transparent and less spongy test, and pigmentation of the living colony. *Distaplia tokioka* n.sp. has similar colonies but its gonads are in a posterior abdomen.

The zooids of *D. dubia* (Oka, 1927c) from Japan and Lord Howe I. (see above, *D. dubia*) most closely resemble those of the present species, but they have more numerous stomach folds, more stigmata and form more regularly circular systems.

Distaplia cuscina n.sp. has more stigmata than the present species, does not form such extensive sheet-like colonies, and has simple, circular cloacal systems and a vertically oriented stomach with conspicuous internal ridges.

Distaplia pallida resembles *Hypsistozoa distomoides* and the New Zealand *H. fasmeriana* — both species having deep rounded stomach folds, a horizontally oriented stomach, and similar numbers of stigmata. However, *Hypsistozoa* spp. have stalked or upright colonies, never sheet-like ones like those of *D. pallida*, and they have conspicuous longitudinal muscles on the posterior abdominal vascular appendix, as well as gonads posterior to the gut loop.

Distaplia prolifera n.sp.
(Fig. 44a,b)

Distribution

Type Locality: Western Australia (11 nautical mls NW Port Hedland, 20°12'S 118°25'E, 14m, coll. L. Marsh on RV *Soela* 5.8.82, holotype WAM 812.83 *QM GH2103*).

Further Records. None.

Description

External Appearance. The single available colony is large and irregular, completely investing a large branching algal stalk. Its maximum dimension is 15cm and its maximum thickness is 1cm. The test is tough and spongy. In preservative it is pink, owing to pink pigment particles embedded in the surface test. Zooids are in circular to oval systems, and in the preserved colonies the surface test is slightly depressed over the systems.

Internal Structure. Zooids are large, being about 4mm long, even with the thorax contracted. They have a long oesophageal neck that is more than half the length of the abdomen. Gonads are in a sac posterior to the abdomen, attached to the right side of the gut loop by a narrow neck. About 34 fine longitudinal muscles are on the

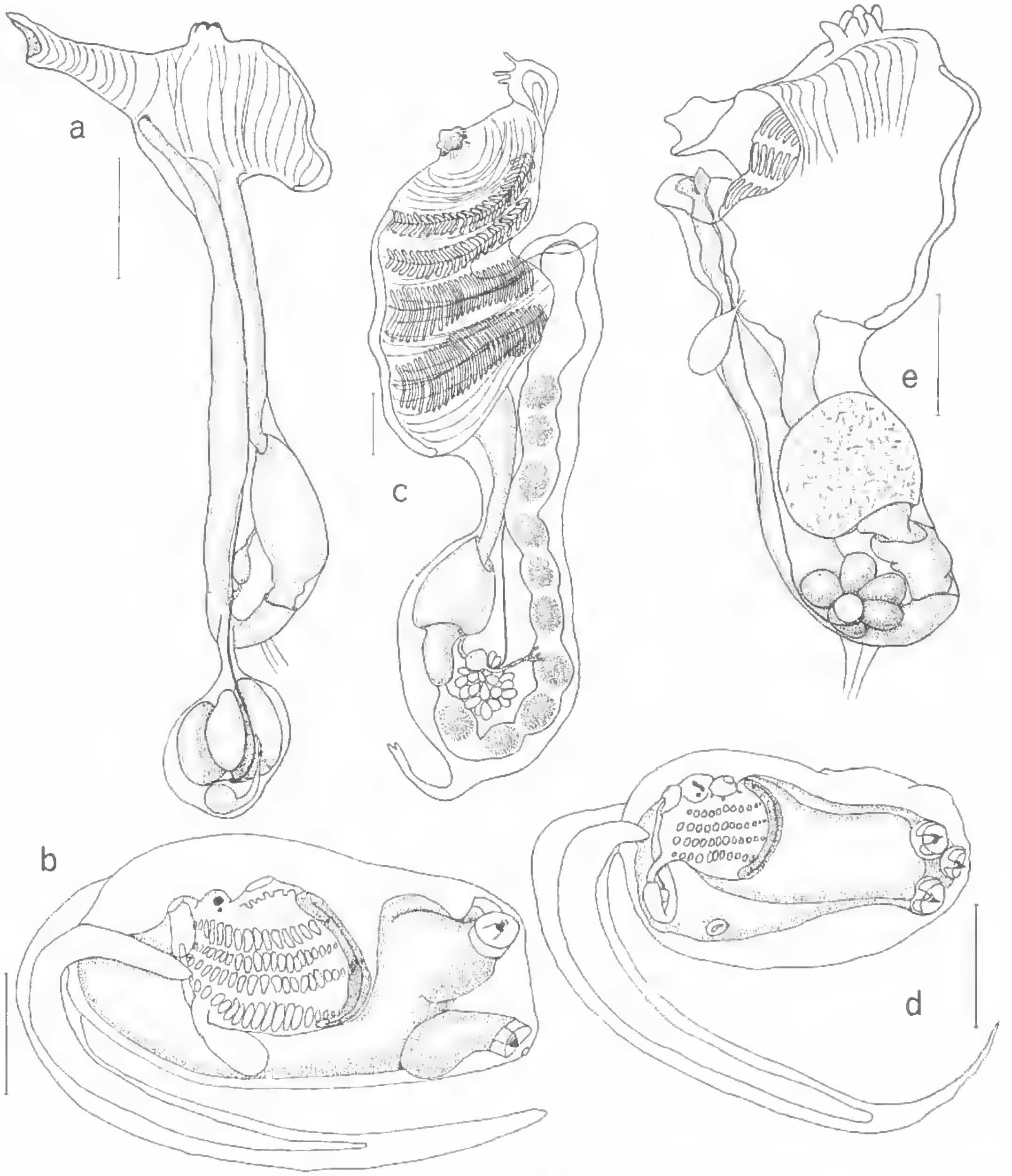


FIG. 44. *Distaplia prolifera* n.sp. (holotype WAM 812.83): **a**, zooid; **b**, larva. *Distaplia racemosa* n.sp. (holotype NTM E9): **c**, zooid; **d**, larva. *Distaplia regina* n.sp. (holotype QM GH4201): **e**, zooid. Scales: **a–e**, 0.5mm.

thorax, including those that cross the dorsal midline between the apertures and continue around the atrial aperture. The branchial aperture is 6-lobed. Sometimes the atrial aperture is wide open exposing the dorsal part of the branchial sac, but sometimes it is produced out on the end of a siphon. There is only a short pointed lip from the upper border of the atrial opening. On the left 18 stigmata are in each of the 3 anterior rows and 16 in the posterior row. On the right 16 stigmata are in the anterior 3 rows and 14 in the posterior row. A parastigmatic vessel crosses each row of stigmata.

The stomach is in the posterior third of the abdomen. The distal end of the oesophagus turns slightly toward the ventral surface before entering the stomach and the oval stomach is itself slightly obliquely oriented. The stomach is not folded, although its internal wall has about 20 fine longitudinal striations in its glandular lining. The mid-intestine opens into the rectum in the pole of the gut loop and there is a distinct rectal valve. A long elliptical gastric reservoir lies in the gut loop.

Four long testis follicles are in the posterior abdomen. They are longitudinally oriented, opening into the vas deferens at their posterior ends. A small ovum is also present at the posterior end of the abdomen near the proximal end of the vas deferens. In this holotype colony, collected in August, there is a single well-developed embryo in each brood pouch. The brood pouches are present in the test behind the zooids, attached to the thorax by a long narrow neck, often hard to distinguish in the rather tough test.

Larvae are large, the oval trunk being 2.2mm long. The tail is relatively short, reaching only to the anterior end of the trunk. There is an otolith and an ocellus in the cerebral vesicle. The large adhesive organs occupy the anterior third of the trunk. Each adhesive organ has a single large balloon-like expansion at the base of its stalk. There are two small buds from the oesophageal region of the oozooid.

REMARKS: Although *Distaplia pallida* n.sp. also has an investing colony and zooids arranged in circular to oval systems, it is distinguished from the present species by the absence of a posterior abdominal sac — its gonads being enclosed in the gut loop. *Distaplia tokioka* n.sp. has investing colonies and gonads in a posterior abdominal sac like those of the present species but its stomach wall is folded. Other species with their gonads in a posterior abdominal sac form stalked colonies that are readily distinguished from the present investing species. Further, both zooids and larvae of *D. violetta* n.sp. and *D. stylifera* are smaller than those of *D. prolifera* n.sp.

Distaplia racemosa n.sp.
(Fig. 44c,d)

DISTRIBUTION

TYPE LOCALITY: Northern Territory (Arafura Sea, Cootamundra Shoals, 10°49′49.966′S 129°12′54.876′E, 36m, coll. R. Lockyer 6.5.82, holotype NTM E9 *QM GH4366*).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony is investing, growing around a narrow woody stem. It is long. The edges have partially joined together along one side so it appears to be a cylinder of about 2cm diameter. Thus the species will probably be found as a flat, investing sheet when taken from other substrates. There are regular circular systems of about 6 zooids. The systems are evenly spaced, the cloacal apertures being about 1cm apart. In the preserved specimen the surface of the colony is depressed over each system.

The colony is firm, owing to the thick (0.5cm) gelatinous and translucent but firm outer layer of test at thoracic level. The inner test around and posterior to the abdomen is soft, spongy and almost opaque, containing the posterior abdominal stolons and developing vegetative zooids. The outer translucent layer of test is pale pink in preservative. The soft inner layer is white.

INTERNAL STRUCTURE: Zooids are about 6mm long. The body wall has conspicuous fine horizontal muscle bands crossing the sides of the body from the endostyle. Short longitudinal bands radiate from the branchial aperture over the anterior end of the thorax to the level of the second row of stigmata. The branchial siphon is short and its border is divided into 6 shallow lobes. The large anterior atrial lip has 3 fine projecting tongues along its terminal edge. This lip is inserted into the test around the cloacal aperture. There are 4 rows of long stigmata, 26 in the anterior 3 rows and 24 in the posterior row. Each row is crossed by a fine parastigmatic vessel. The oesophagus is long and narrow. The relatively short, smooth-walled and slightly obliquely oriented stomach is about halfway down the abdomen. There is a small oval posterior stomach. The gut loop encloses a spherical mass of short, only slightly pyriform testis follicles. A single ovum is present on the right side of the testis at the base of the vas deferens.

Embryos and tailed larvae are present in the test at oesophageal level, the stalk of the brood pouch being relatively short. Only a single embryo develops in each brood pouch. Larvae have a trunk 1.8mm long and a relatively short tail reaching about halfway around the trunk. They have an ocellus and a small otolith. The triradially arranged adhesive organs have short stalks that are not expanded at their base.

REMARKS: Only the holotype colony is available. Its size and its well-separated and evenly distributed circular systems are distinctive, as is the outer firm gelatinous layer of test that is of entirely different consistency from the basal test. The zooids with their predominantly transverse musculature most closely resemble those of the Japanese *D. systematica* Tokioka, 1958 (described from a single colony) and the possibly conspecific specimen from Toeal (specimen 2.iii.1922) assigned to *D. stylifera* by Millar (1975). Tokioka's (1958) specimen had no gonads. The testis in the colony from Toeal is not the same spherical mass of crowded male follicles as that found in the present species. Further, both Japanese and Toeal material consist of separate stalked lobes, arising from a common base, each lobe containing a single circular system. Although it is possible these colonies are juveniles, and each lobe could develop to accommodate numerous circular systems (as in the present species), the growth pattern, in which additional lobes are added to the colony, appears different from the sheet-like *D. racemosa*.

The circular systems and the zooids of the present species resemble those of *D. viridis*, although the longitudinal thoracic muscles are more conspicuous in the latter species and it has more stigmata.

The relatively numerous branchial stigmata and the sheet-like form of the colony are characters shared with the temperate species *D. florida* which, however, has more crowded circular systems and larvae with numerous ectodermal ampullae at the anterior end of the trunk. The relatively large larvae of the present species, without expansions at the base of the adhesive organs, are characteristic.

Distaplia regina n.sp.

(Fig. 44e)

Distribution

Type Locality: Queensland (Heron I., Capricorn Group, low tide, under side of rubble, coll. P. Kott 25.5.87, holotype QM GH4201; paratype QM GH4202).

Further Records: None.

Description

External Appearance: Colonies are soft and irregular cushions 2 to 3cm in maximum diameter and less than 5mm thick. Zooids are arranged in circular systems around sessile cloacal apertures. Living colonies are dark purple with clouds of white particles in the surface test. These are concentrated over the atrial lips to form a white patch in the centre of each system in the vicinity of the cloacal aperture. Immediately on fixation with formalin the colour of the colony changes to, and remains, cloudy pink. Dark red-brown pigment cells were in the test after a period in preservative. The test has the spongy consistency of so many species of this genus.

Internal Structure: Zooids are about 3mm long when contracted. They are almost opaque in preservative, with a greenish translucent stomach and proximal part (descending limb) of the intestine. There are 6 pointed branchial lobes. The atrial opening is large with a long anterior lip and 3 tongues on its outer lip. About 15 longitudinal thoracic muscles extend from the branchial siphon. Other fine muscles cross the mid-line dorsal to the branchial siphon, some curving out into the atrial lip and then continuing down each side of the atrial aperture. No oblique or transverse muscles originating from the ventral mid-line were observed in these zooids.

The stigmata are moderately long and rectangular, but no parastigmatic vessels were detected in these specimens. On the right side of the branchial sac are 20 stigmata in each of the 3 anterior rows and 18 in the posterior row; and on the left 18 in each of the anterior rows and 16 in the posterior row.

The abdomen is relatively large, the gut being especially voluminous. The large stomach is about halfway down the abdomen, more or less vertically oriented in the vertical gut loop. It is spherical or slightly oblong. Externally its wall is smooth but internally the glandular epithelium is raised in short ridges or papillae to form a reticular pattern when seen from the outside. The short ridges are oblique or transverse, seldom longitudinal. A short duodenal area narrows before it enters the rectum, where there is a distinct rectal valve. The gut loop encloses a circle of about 5 club- to wedge-shaped testis follicles. These join the vas deferens in the centre of the circle. A single egg is sometimes present near the proximal end of the vas deferens. It projects slightly from the side of the abdomen. There is a rudimentary brood pouch attached by a narrow neck to the postero-dorsal corner of the thorax just to the right of the mid-line. No embryos were being brooded in either the holotype or paratype colony.

Remarks: Although the soft cushion-like colony, the systems, and the numbers of stigmata present in this species resemble those of *D. cuscina* n.sp., zooids are larger and the gut, especially the almost spherical, roomy stomach with its unique internal pattern and greenish translucent colour, are distinctive. *Distaplia yezoensis* Tokioka, 1951a, from Japan, has both colony and zooids (including the reticular pattern in the internal stomach lining) that resemble those of the present species. The Japanese species has fewer stigmata (12 to 13) and it has conspicuous parastigmatic vessels. It appears to be a separate species.

Distaplia retinaculata n.sp.

(Fig. 45)

Distribution

Type Locality: Victoria (1.5km off McGauran's Beach, Ninety Mile Beach, reef 15m coll. J.E. Watson

R7F/8 1977, holotype MV F53267 *QM GH4127*; R3F/44 paratype MV F53268).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are soft, fleshy, cylindrical and rope-like, up to 1cm in diameter. In all recorded specimens much of the surface of the colony appears to be disintegrating, and systems are disrupted. However, there are entire areas where zooids are in crowded circular systems of about 12 around large common cloacal apertures up to 2mm in diameter. Some dark grey pigment particles are present in the surface test of the preserved colonies. The soft centre of the cylindrical colony is filled with a tangle of fine vascular processes.

INTERNAL STRUCTURE: Zooids are about 4mm long. The branchial aperture is 6-lobed. The atrial aperture is wide with a pronounced lip from its upper border. The free terminal border of the atrial lip is divided into 3 or 4 small tongues. Longitudinal and oblique muscles are on the thorax, and fine fibres extend along each side of the abdomen. The branchial sac has 20 stigmata in the anterior rows and 18 in the posterior row. A fine parastigmatic vessel extends across each row of stigmata.

The oesophageal neck is rather long, being more than half the length of the abdomen. There is no posterior abdominal sac. The vertical, oval stomach, in the anterior half of the posterior third of the abdomen, is smooth externally. Internally it has numerous fine and mostly longitudinal striations in its glandular wall. A short, broad mid-intestine posterior to the stomach opens into the wider rectum. The proximal part of the rectum curves around to form the pole of the gut loop. Gonads, consisting of a circular to hemispherical mass of about 10 pear-shaped male follicles and a large ovum are present just to the right of the posterior end of the gut loop. The vas deferens makes a loop over the surface of the ovum. Gonads are present in the vegetatively produced zooids, which are present in the test between the adult zooids. In these vegetative zooids the ovum protrudes from the side of the abdomen and is connected to it by a narrow stalk. Large yellowish embryos(?) lie free in the test in the centre of the colony. They do not appear to be in a brood pouch and probably rupture from the abdomen into the test, presumably after fertilisation.

In most of the zooids there are two vascular processes from the left side of the gut loop.

REMARKS: This species most closely resemble *Distaplia cylindrica* (Lesson) from the Antarctic (see Kott 1969) which also often is found in a similar disintegrated condition. The Antarctic species has more numerous stigmata in the branchial sac and distinct ridges in the stomach wall. Although it has not been reported for the present species, it is possible that the long cylindrical zooid-bearing heads break away from the substrate and float near the surface of the sea as the Antarctic species is known to do (Kott 1969).

Although their colonies are distinctive, the zooids of the present species most resemble those of *D. viridis* which also have a smooth stomach, the same numbers of stigmata, similar circular systems and an ovum projecting in a sack from the side of the gut loop in small vegetatively produced zooids.

The brooding of the embryos in the test, and their release directly from the abdomen is a phenomenon associated with large eggs. It always occurs in the Didemnidae and in the genera *Hypodistoma* and *Polydistoma* n.gen. It is not known to occur in any other species of *Distaplia*. The larva is not known for this species.

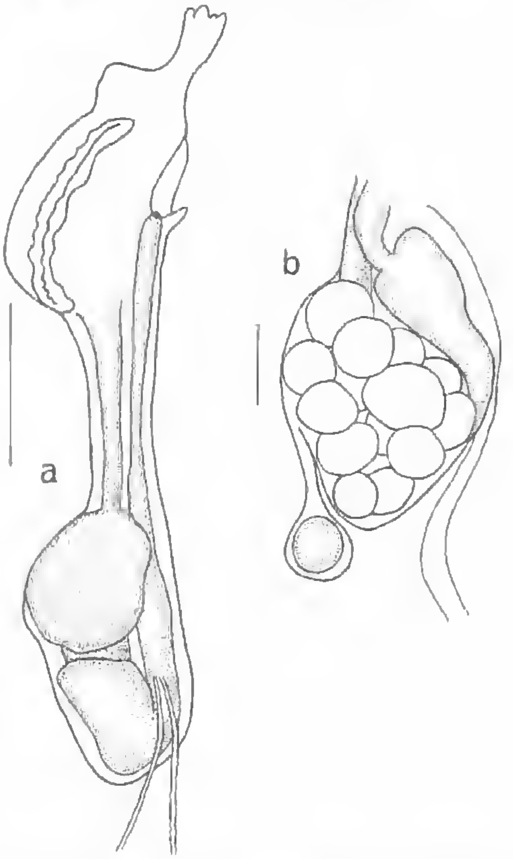


FIG. 45. *Distaplia retinaculata* n.sp. (holotype MV F53267): a, zooid; b, abdomen of vegetative zooid with precocious gonads. Scales: a, 1mm; b, 0.25mm.

Distaplia stylifera (Kowalevsky, 1874)
(Fig. 46. Plate 9f,g)

Didemnium stylifera Kowalevsky, 1874, p. 443.
Distaplia stylifera: Michaelsen, 1930, p. 502. Brewin, 1953, p. 60. Kott, 1957a, p. 95; 1972b, p. 170. Millar, 1963a, p. 713; ? 1975, p. 224 (part, ZMC, 19.iv.1922 from Toeal). ? Monniot, 1988, p. 197.
Distaplia magnilarva: Seeliger, 1907, p. 1018.
Distaplia mikropnoa: Hartmeyer, 1919, p. 130. Tokioka, 1955a, p. 51; 1967a, p. 130.

Distribution

New Records: Western Australia (Houtman's Abrolhos, WAM 808.83; Shark Bay, WAM 809 11.83; Triggs I., WAM 33.72 14 5.84; Cockburn Sound, WAM 40.72 69.75 140.75 142.75 207.75 22.84). South Australia (Great Australian Bight, QM GH943 GH970 GH2292 GH2302 GH2407). Queensland (Hervey Bay, QM GH4129; Wistari Reef, QM GH4132; Heron I., QM GH4203).

Previously Recorded: Western Australia (Broome, Roebuck Bay Millar 1963a. Cape Jaubert Hartmeyer 1919; Shark Bay Michaelsen 1930; Cockburn Sound Brewin 1953, AM Y1180 Y1185 Kott 1957a, Millar 1963a). South Australia (Great Australia Bight SAM E1997 Kott 1972b). Palau Is (Tokioka 1955b, 1967a). ? Philippines (Millar 1975). Red Sea (Kowalevsky 1874).

It is surprising that with such a wide range the species has been recorded only twice from the eastern coast of Australia, and not at all from the western Pacific Ocean. The Queensland records are of a specimen cast up after a stiff northerly gale (*fide* G. McKoen, QM GH4129) and two orange-vermilion (Ridgeway 1886) colonies from the Capricorn Group (QM GH4132 GH4203).

Description

External Appearance: Colonies are mushroom- or toadstool-shaped, the zooid bearing head being rounded to conical and the stalk short and fleshy. Sometimes a number (up to 6) of heads branch off the top of a common stalk or they arise from a common basal mass of test. The stalk is often cylindrical and the base of the zooid-bearing head may overlap it. In other colonies the stalk expands at the top and its junction with the head is not sharply defined. The zooids are arranged in circular, oval and long radiating double row systems all over the head. The common cloacal apertures have 5 or 6 lobes. The test is firm and of a spongy consistency.

Living colonies are pink-red, orange vermilion (Ridgeway 1886) or beige with golden zooids. The colony cast up on the Queensland coast is reported to have been a rich orange. In preservative all colonies are the same beige colour, although sometimes a trace of red pigment is present in parts of the zooids.

Internal Structure Zooids are about 3mm long, excluding the posterior abdominal sac that contains the gonads. The branchial apertures are 6-lobed. The atrial apertures are wide with an anterior lip that is pointed or flattened with 2 to 5 small teeth projecting from its terminal border. There are about 30 longitudinal and oblique thoracic muscles, and more variation in the number of stigmata in each row than is usual in this genus. In specimens from Western Australia, South Australia and Queensland, respectively, the maximum number (in the left anterior rows) is 18, 16 and 14. There are, as usual, 2 stigmata less in the posterior rows than in the anterior rows; and 2 more in rows on the left than in corresponding rows on the right. Parastigmatic vessels were not detected in any of the specimens except the one from Hervey Bay (QM GH4129).

The oesophagus bends ventrally to enter the shield-shaped stomach which has a long curved ventral border and a much shorter dorsal border. The stomach has 16 to 20 distinct curved, longitudinal folds, some of which branch. A large oval gastric reservoir lies in the gut loop. The mid-intestine is separated from the rectum by a distinct rectal valve.

Gonads are present in a small sac behind the abdomen, although it does not always have a particulary narrow neck separating it from the abdomen. The testis consists of a grape-like cluster of up to 15 pear-shaped follicles. Often a large ovum lies alongside the testis. The vas deferens extends over the surface of the ovum in a convoluted course. In one Queensland specimen (QM GH4203) there are only 6 wedge shaped male follicles crowded together in a circle. In this specimen the posterior abdomen is connected to the left side of the abdomen by only a short neck. This specimen and some from north western Australia (WAM 977 8.83) have the triangular body that was described by Tokioka (1967a) alongside the ascending limb of the gut loop. It is yellowish and translucent. It does not appear to be part of the gastric gland, as Tokioka suggested.

A single embryo is in the relatively short-necked brood pouch in specimens collected from Western Australia in January (WAM 22.84), April (WAM 809.83) and December (WAM 140.75). However, other specimens collected in those and other months from both Western Australia and South Australia do not have embryos.

Larvae have an almost spherical trunk, 1.2mm long and only slightly longer than deep. The whole stalk of each adhesive organ appears expanded

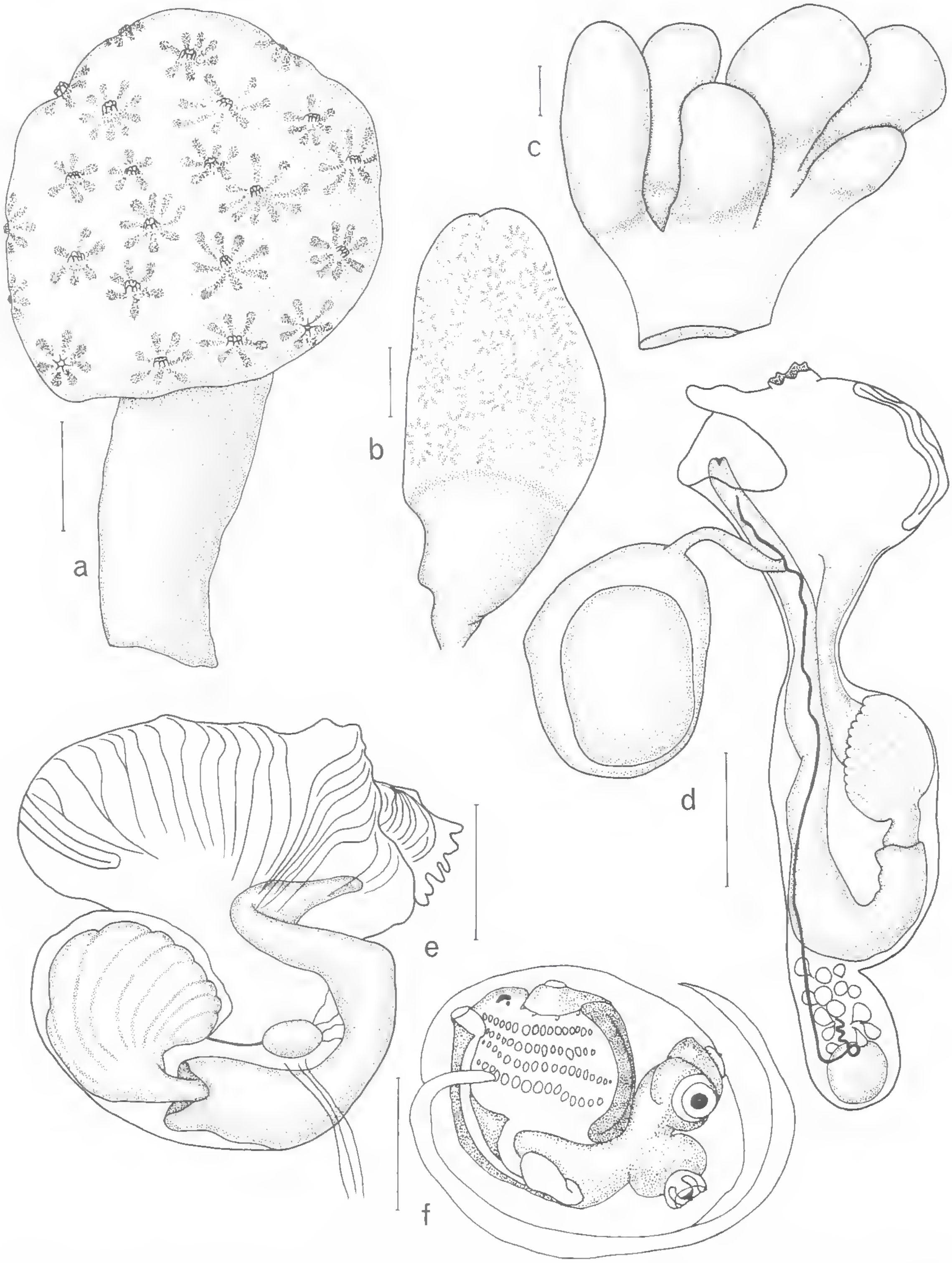


FIG. 46, *Distaplia stylifera*: **a–c**, colonies (QM GH2407, WAM 810.83 808.83); **d,e**, zooids (WAM 808.83, QM GH2292); **f**, larva (WAM 810.83). Scales: **a**, 5mm; **b,c**, 1cm; **d–f**, 0.5mm.

into a balloon-shape. There is an ocellus and an otolith in the cerebral vesicle.

Remarks: Michaelsen (1930) believed that *D. bursata* (Van Name, 1921) from the West Indies was a synonym of *D. stylifera* from the Red Sea and north-western Australia, and other authors have followed him in this. Although the colonies and even the pigmentation as well as some characteristics of the zooids including the numbers of stigmata are identical, the West Indian species has a narrow-necked posterior-abdominal sac containing only 6 long testis follicles that more closely resemble those of *D. australiensis* than the usually numerous, shorter follicles of the present species.

Some of the specimens from the Philippines (ZMC 19.iv.1922) with stalked colonies, circular systems and bunched testis follicles that were referred to *D. stylifera* by Millar (1975) probably do belong to this species, although other specimens have the parastigmatic vessels, several embryos in the brood pouch and the longer larval trunk of *D. violetta* n.sp. Specimens from New Caledonia assigned to *D. stylifera* by Monniot (1988) may also belong to *D. violetta* n.sp. They have parastigmatic vessels, few male follicles, circular systems and are grey-green (in preservative?).

Tokioka (1955b, 1967a) used the absence of parastigmatic vessels to distinguish *D. mikropnoa* (Sluiter, 1909) from *D. stylifera*. However, parastigmatic vessels were not recorded in the type of *D. stylifera* from the Red Sea and as the species has not been taken since from that location it is not possible to confirm their absence. Parastigmatic vessels are not present in specimens assigned to both *D. stylifera* and *D. mikropnoa* from Western Australia, Indonesia and the Palau Is (see Sluiter 1909, Hartmeyer 1919, Michaelsen 1930 and Tokioka 1955b, 1967a). In specimens assigned to both species (see synonymy, above) the male follicles usually are numerous, short, pear-shaped and bunched together, although in some specimens (like those described by Michaelsen 1930) there are as few as 6 relatively large wedge-shaped follicles crowded together in a ring (see also QM GH4203). Thus, neither the presence nor absence of parastigmatic vessels nor the number of male follicles afford a means of distinguishing between *D. mikropnoa* and *D. stylifera*.

In fact, most of the specimens assigned to *D. mikropnoa* appear to be conspecific with *D. stylifera*. *Distaplia mikropnoa* (> *Polyclinum mikropnous* Sluiter, 1909) appears a distinct species separated from *D. stylifera* by its colony form, long oval stomach oriented in the longitudinal axis of the body, and branching network of stomach folds. The type specimen is a large sponge-like mass 4cm wide, 6cm long and up to 8mm thick — different from the stalked upright colonies that characterise *D. stylifera*.

Some of the larger colonies resemble those of *Hypsistozoa distomoides* which also has a thick, fleshy stalk. In the absence of the characteristically located gonads, *H. distomoides* can be distinguished by the conspicuous muscles on its vascular process and its less numerous stomach folds. The convoluted course of the proximal part of the vas deferens in the present specimens is similar to that in *D. retinaculata* n.sp.

Distaplia tokioka n.sp.

(Fig. 47a,b)

Distribution

Type Locality: South Australia (Great Australian Bight, Price I., Avoid Bay, 15–20m, coll. N. Holmes 9.4.87, holotype SAM E2081, paratypes GH4179).

Description

External Appearance: The type material consists of numerous sessile, irregularly shaped cushion-like colonies, up to 5mm thick and 6cm in maximum dimension, investing weed stalks and fronds. Zooids are arranged in circular systems. Common cloacal apertures, about 5mm apart, protrude from the surface as rounded prominences, their borders entire, and not divided into lobes. The test is firm, with the usual spongy consistency of most species of this genus.

Internal Structure: Contracted zooids are about 2mm long excluding the posterior abdominal sac which is connected to the abdomen by a short but narrow neck. There are 6 well defined triangular branchial lobes. The atrial aperture has the usual large anterior lip with 2 or 3 pointed terminal processes. Thoracic muscles are conspicuous, and appear all longitudinal, about 20 extending from around the branchial siphon, and additional bands curving out into the atrial lip and down along each side of the aperture. The branchial sphincter is well developed.

On the right are 16 stigmata in the anterior 3 rows and 14 in the posterior row, and on the left 14 and 12 respectively. Parastigmatic vessels are present. The oesophagus bends ventrally to enter the almost horizontal and rather long stomach, which has about 12 longitudinal folds in its wall. A conspicuous spherical gastric reservoir lies in the rather wide gut loop.

Gonads are not mature in these specimens. However, some zooids have small, tear-drop-shaped posterior abdomina, attached by a relatively long narrow neck, to the right side of the abdomen. They contain small, pear-shaped testis follicles.

Remarks: Externally, this species resembles *D. viridis* and *Distaplia pallida* n.sp. Although the individual colonies are not as extensive, their shape may be affected by the substrate, in this case weed fronds and stalks. Further, the geographic range of both *D. viridis* and *D. pallida* includes the type locality of the present species. However, although *D. pallida* has a similar number of gastric folds, it is readily distinguished by the presence of the gonads in the abdomen rather than in a posterior abdominal sac. *Distaplia viridis* has similar circular systems and conspicuous protruding cloacal apertures, but also has gonads in the abdomen rather than in a posterior abdominal sac, and it has more stigmata and lacks stomach folds.

Amongst the species that do have a posterior abdominal sac, the tropical *Distaplia violetta* n.sp. resembles the present species in its circular systems and number of stomach folds. However, it has thicker colonies, conspicuously lobed cloacal apertures and more numerous stigmata.

Distaplia stylifera, with similar short male follicles bunched in the posterior abdomen, and often simple circular systems as in the present species, has more numerous stigmata and stomach folds, and lacks parastigmatic vessels. Further although there are many paratype colonies of the present new species, not one of them has the stalk that usually is characteristic of *D. stylifera*. *Distaplia prolifera* has a smooth stomach with longitudinal striations internally and only 4 long male follicles.

Distaplia violetta n.sp.

(Fig. 47c–e)

? *Distaplia stylifera*: Millar, 1975, p. 224 (part, specimens ZMC 17 22.iii.1914). Monniot, 1988, p. 197.

Distribution

Type Locality Queensland (Capricorn Group, Wistari Reef, low tide rubble fauna, coll. P.K. 5.8.82, holotype QM GH1358; Heron I coll. P.K. May 1985, paratypes QM GH4130, May 1987, QM GH4204).

Further Records Queensland (Capricorn Group, QM GH4131 GH4133 GH4135 7 GH4205 9 GH4439; Townsville, QM GH4138). ? Philippines (Millar 1975). ? New Caledonia (Monniot 1988).

Description

External Appearance: Colonies are small, sessile flat-topped platforms about 1cm high, with thick basal test, and with the wide, flat, upper surface narrowing toward the base and sometimes forming a short fleshy stalk. Zooids are in circular systems around conspicuous projecting cloacal apertures with 5-lobed rims. Each system is about 4mm in diameter. Zooids are always vertical and parallel to one another, opening only on the top and never on the sides of a colony. The test has a spongy consistency.

The colour of the living colonies results from mixtures of dark 'pansy purple' (Ridgeway 1886) pigment cells with clouds of opaque white particles in the surface test. Sometimes some yellow or brown pigment is also in the centre of the cloacal systems. Thus resulting colours vary, being flesh-coloured, blue, mauve with pink, plum coloured test with pink zooids. In preservative, colonies are green, with indigo blue pigment cells in the surface test and green in the remainder of the test.

Internal Structure: Zooids are less than 3mm long, excluding the posterior abdominal sac which is joined to the right side of the posterior end of the abdomen by a fairly long, narrow neck. The thorax is longer than the abdomen. The branchial lobes are large and triangular, those on the ventral part of the opening projecting in front of the dorsal ones. The atrial aperture is the usual wide opening, although it is sometimes produced forwards into a funnel-shaped siphon protecting the branchial sac from direct exposure to the cloacal cavity. A pointed lip is produced from the anterior rim of the atrial aperture. There are about 20 fine longitudinal muscle bands on the thorax some extending across the dorsal mid-line between the apertures and curving out into the atrial lip. On the left are 20 stigmata in each of the anterior 3 rows and 18 in the posterior row; on the right, are 18 and 16 respectively. Parastigmatic vessels are present.

The oesophagus bends ventrally to enter the curved stomach about halfway down the abdomen. The stomach has 8 to 12 folds that flatten out toward the pyloric end, where the diameter of the stomach decreases. These are true stomach folds rather than internal ridges, as the whole stomach wall is folded. There is a short, narrow mid-intestine and a distinct rectal valve where the intestine opens into the rectum in the pole of the gut loop.

A tight group of 4 to 6 relatively short, wedge-shaped male follicles is in the posterior abdominal sac. Three small ova are often at the outer end of the male follicles where they join the vas deferens. A single, well-formed embryo is present in the long-necked brood pouches of some of the specimens collected in May (QM GH4208), August (QM GH1358 GH4439) and November (QM GH4137) from the Capricorn Group. In one colony up to 2 large eggs were in each brood pouch, as well as a well advanced larva. No embryos were

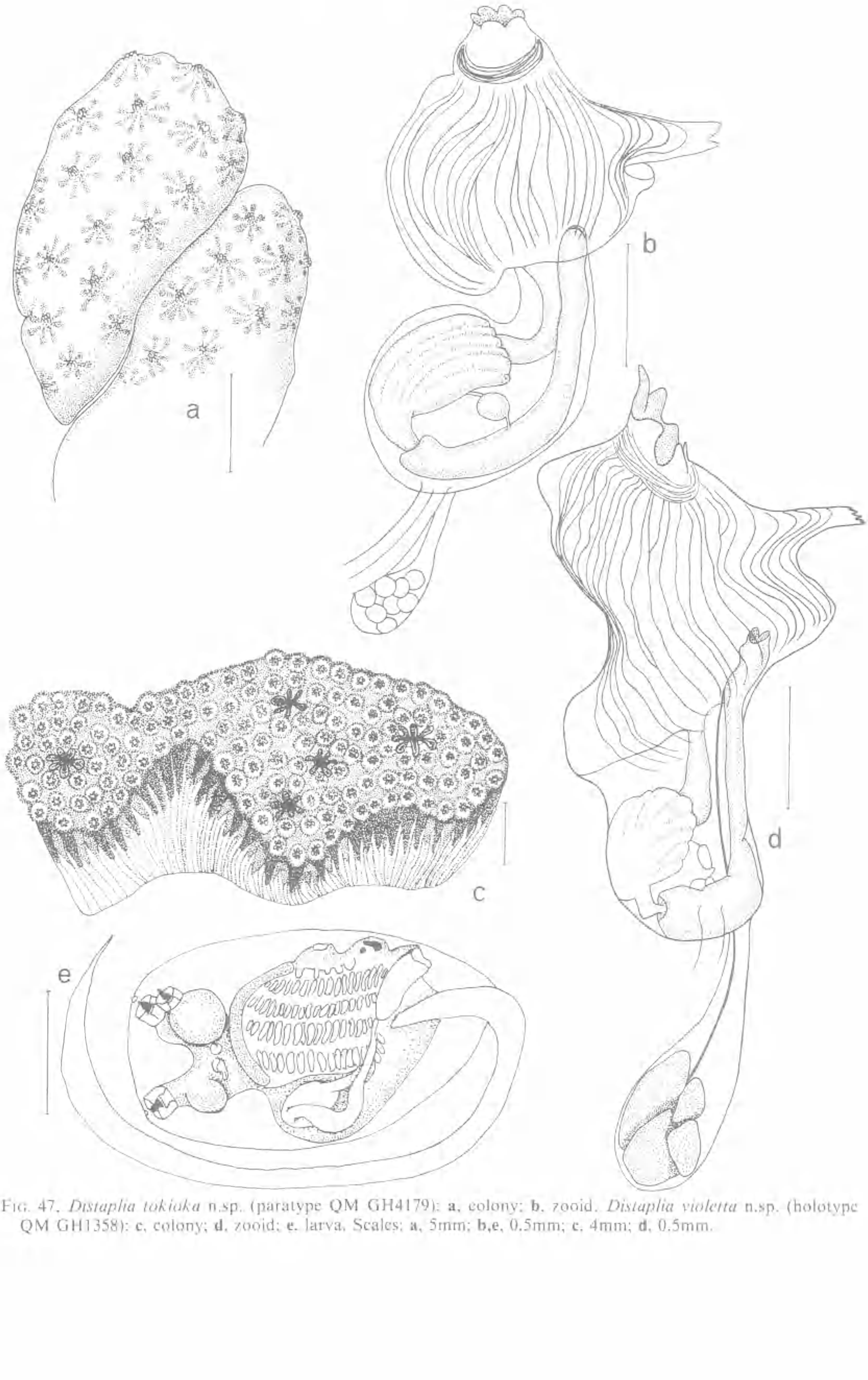


FIG. 47. *Distaplia tokioka* n.sp. (paratype QM GH4179): **a**, colony; **b**, zooid. *Distaplia violetta* n.sp. (holotype QM GH1358): **c**, colony; **d**, zooid; **e**, larva. Scales: **a**, 5mm; **b,e**, 0.5mm; **c**, 4mm; **d**, 0.5mm.

present in January or June. The length of neck of the brood pouch is variable. Sometimes brood pouches are near the base of the colony, suspended from the posterior part of the thorax by long, narrow necks.

The larval trunk is 1.6mm long, and the tail is relatively short, reaching halfway around the trunk. There is a well-formed ocellus and otolith. The base of the stalk of each of the 3 adhesive organs is expanded but ampullae are not developed. The hyaline cap on the axial cone is large, conspicuous and appears detached. Two blastozooids lie in the frothy looking larval test.

REMARKS. This species is readily confused with *D. stylifera*. *Distaplia violetta* can be distinguished by its less conspicuous and less numerous stomach folds, longer larval trunk, occasionally more than one embryo in the long-necked brood pouch, and the plum colour of its living colonies and their dark and subsequently greenish colour in preservative. The testis follicles of *D. stylifera* are usually (but not always) smaller and more numerous. The specimens with parastigmatic vessels and several long embryos in the brood pouch assigned to *D. stylifera* by Millar (1975) may be of this species.

Living colonies resemble those of *D. cuscina* n.sp. but have more conspicuous cloacal apertures, and zooids are readily distinguished by the posterior abdomen of *D. violetta*.

Zooids resemble those of *D. tokioka* n.sp. from South Australia, although the upright, flat-topped colonies of the present species are distinctive and its zooids have fewer and larger male follicles and more stigmata.

Distaplia viridis Kott, 1957
(Fig. 48, Plate 10a–c)

Distaplia viridis Kott, 1957a, p. 96; 1972a, p. 7 (part, specimens from Port Noarlunga, fig. 7). Millar, 1966a, p. 365.

Not *Distaplia viridis*: Kott 1972a, p. 7 (part, fig. 6 specimens from Hallett Cove < *Distaplia pallida* n.sp.)

DISTRIBUTION

NEW RECORDS. South Australia (Great Australian Bight, SAM E2040, QM GH4146 GH4159; Spencer Gulf, QM GH4216). Victoria (Portland, QM GH45). Queensland (Heron I, QM GH4385).

PREVIOUSLY RECORDED. South Australia (Spencer Gulf — Y2069 Kott 1957a; St Vincent Gulf — AM Y1182 Y2070 Kott 1957a, SAM D239 Kott 1972a). Victoria (Port Phillip Bay — Millar 1966a).

The species appears indigenous most often taken from the coastal area between Spencer Gulf and Port Phillip Bay down to 8m. It is presumed the single record from Heron I. represents the northern limit of its range.

DESCRIPTION

EXTERNAL APPEARANCE. Colonies are flat cushions up to 1cm in thickness with the zooids opening only on the flat top of the colony. Zooids are arranged in circular systems of up to 10 around a central conspicuous and protruding cloacal aperture. In preserved material the surface test is slightly depressed over these systems, which are about 4mm in diameter. Living specimens have been described as brown and white, blue-black with white markings, whitish with purple pigment around systems, and blue-grey reticulate pattern, the latter created by darker pigment around the circular systems. In preservative colonies are usually cream with a greenish tinge, although some dark bluish pigment granules are sometimes in the relatively thin test over the systems. The colony from Heron I. is greenish blue over the systems and dark blue between them, although the colour

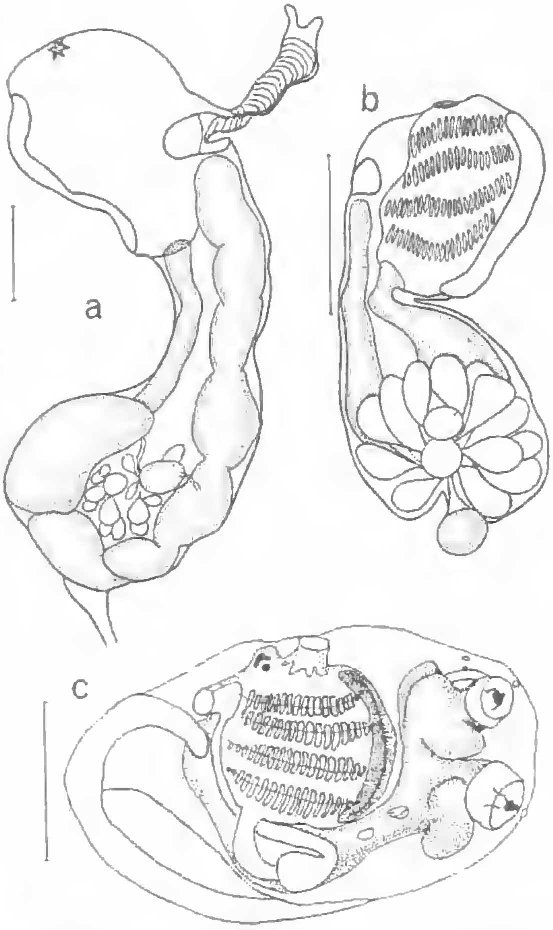


FIG. 48. *Distaplia viridis*: a, adult zooid (QM GH45); b, vegetative zooid with precocious gonads (QM GH45); c, larva (AM Y1182). Scales: a–c, 0.5mm.

recorded for the living specimen was 'black with white markings' — different from other species occurring at this location, and the same as the South Australian specimens.

INTERNAL STRUCTURE Zooids are not more than 2mm long, the thorax and the abdomen of equal length. A vascular appendage extends from the posterior end of the abdomen, but there is no posterior abdominal sac. The terminal branchial aperture has only small lobes. The upper border of the atrial aperture is produced into a long lip, usually with 2 or 3 small projections at the tip. About 40 fine longitudinal muscles on the thorax extend across the mid-line between the apertures. The most dorsal muscles curve out into the long atrial lip, others radiate from the branchial aperture, and the most ventral muscles (about half of the total number) extend obliquely across from the endostyle to the posterior end of the thorax. Muscles are inconspicuous on the abdomen.

The right side of the branchial sac has 18 stigmata in each of the 3 anterior rows and 16 in the posterior row, on the left 20 and 18 respectively. Parastigmatic vessels are present. The oesophagus is long and narrow, the orange stomach in the posterior third of the abdomen is vertically oriented and slightly kidney-shaped. It has fine reticulations on the surface but no ridges or folds. There are no other apparent subdivisions of the gut. A long oval gastric reservoir is in the gut loop, about halfway along the gastro-intestinal duct that connects the proximal part of the intestine with the middle of the stomach. Gonads are in the gut loop. The species is protandrous. Even small, non-functional, vegetatively produced zooids have large maturing testis follicles on the right side of the gut loop. These small vegetatively produced zooids also have a small ovum projecting from the body wall in the middle of the testis. The testis consists of a circle or hemisphere of pear-to club-shaped follicles converging to the proximal end of the vas deferens in the centre of the circle.

Colonies collected from Spencer Gulf (Kott 1957a) in December have a single large embryo in the brood pouch attached to the postero-dorsal corner of the thorax by a narrow neck. Colonies collected in July from Portland (QM GH45) contain vegetatively produced zooids with maturing testes in both juvenile replicates and adult zooids. Mature eggs and embryos are present in colonies collected from St Vincent Gulf in November (AM Y1182 Kott 1957a).

Larvae are large, with a long cylindrical trunk 1.5mm in length and a relatively short tail about the same length. In mature larvae each relatively narrow stalk of the triradially arranged adhesive organs has at least 2 swollen, balloon like ampullae at its base. Each epidermal concavity, with its cone of adhesive cells in the centre, is rather wide and shallow.

REMARKS The sheet-like colonies of *Distaplia pallida* n.sp. can be confused with those of the present species. However *D. viridis* has thicker colonies, smaller more consistently circular systems of zooids, more numerous branchial stigmata, and a straight, vertical (rather than bent) gut loop. Further, the stomach of *D. pallida* is short and folded while that of the present species lacks folds. In fact, the species that resembles the present one more closely is *D. retinaculata* which, although its colony is completely different, has a similar number of stigmata, circular systems, and the stomach wall smooth externally and with reticulations internally. *Distaplia florida* n.sp. is distinguished from *D. viridis* by its cushion-like colony, its paler pigmentation, its very much larger larva with a more elaborate adhesive apparatus, and its more numerous stigmata. *Distaplia cuscina* n.sp. also resembles the present species having circular systems, a similar number of stigmata, similar gonads, and similar small zooids with longitudinal and oblique muscles. The internal ridges in the stomach and more numerous muscle bands distinguish it from the present species.

Genus **Hypsistozoa** Brewin, 1956b

Type species: *Distaplia fasmeriana* Michaelsen, 1924

The genus contains species closely related morphologically to those of *Distaplia*. Colonies have a zooid-bearing head on a short, fleshy stalk. Zooids are arranged in cloacal systems. The branchial apertures are 6-lobed. The atrial apertures are wide exposing much of the branchial sac to the cloacal cavities, and they have a large anterior lip. There are 4 rows of long, rectangular stigmata, each row crossed by a fine parastigmatic vessel. The abdomen is short, and there is a large gastric reservoir in the loop of the gut, and a rectal valve at the proximal end of the rectum. Gonads are posterior to the gut loop in the top of the conspicuous vascular stolon. Fine longitudinal muscle fibres extend onto and along the vascular stolon. One or 2 embryos develop in a brood pouch connected to the dorsal border of the thorax just behind the atrial aperture, near the terminal part of the rectum. In both *Hypsistozoa fasmeriana* and *H. distomoides* the vas deferens curves posteriorly before extending anteriorly to the atrial cavity, as in some species of *Distaplia* (*D. retinaculata*, *D. stylifera*). Brewin (1959) has described the prolific larval blastogenesis in the type species. Unfortunately mature larvae are not available in any of the known colonies of *H. distomoides* and this cannot yet be confirmed as a character of the genus.

The genus is separated from *Distaplia* by the position of the gonads, and by the well developed vascular stolon with conspicuous muscle fibres extending along it.

In addition to the type species (which is known from New Zealand) and *H. distomoides*, only one other species of this genus is known — *Hypsistozoa obscura* Kott, 1969 from the Peru-Chile Trench. Otherwise the genus appears confined to southern temperate waters.

Hypsistozoa distomoides (Herdman, 1899)

(Fig. 49, Plate 10d–h)

Amaroucium distomoides Herdman, 1899, p. 72.
Aplidium distomoides: Kott, 1957a, p. 95.
Distaplia distomoides: Kott 1972b, p. 170; 1972d, p. 243.

DISTRIBUTION

NEW RECORDS: South Australia (Great Australian Bight, QM GH969 GH1280 GH1294 GH2390 GH4178; Ward I., QM GH1297; Spencer Gulf, GH4182; Yorke Peninsula, SAM E1987; Cape Jervis, QM GH114). New South Wales (Jervis Bay, QM G10044 GH52; Port Kembla, QM G9265 GH2004).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — SAM E1994 6 Kott 1972b). New South Wales (Port Jackson — Herdman 1899, Kott 1972d).

It is a temperate species, and is taken down to 20m. At present it has a discontinuous range, with a gap between its South Australian and New South Wales records.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of a long oval head, up to 4cm long and 3cm in diameter, tapering to a short fleshy stalk. Zooids are arranged in rather crowded circular to long systems of up to 20 zooids. The test is soft and

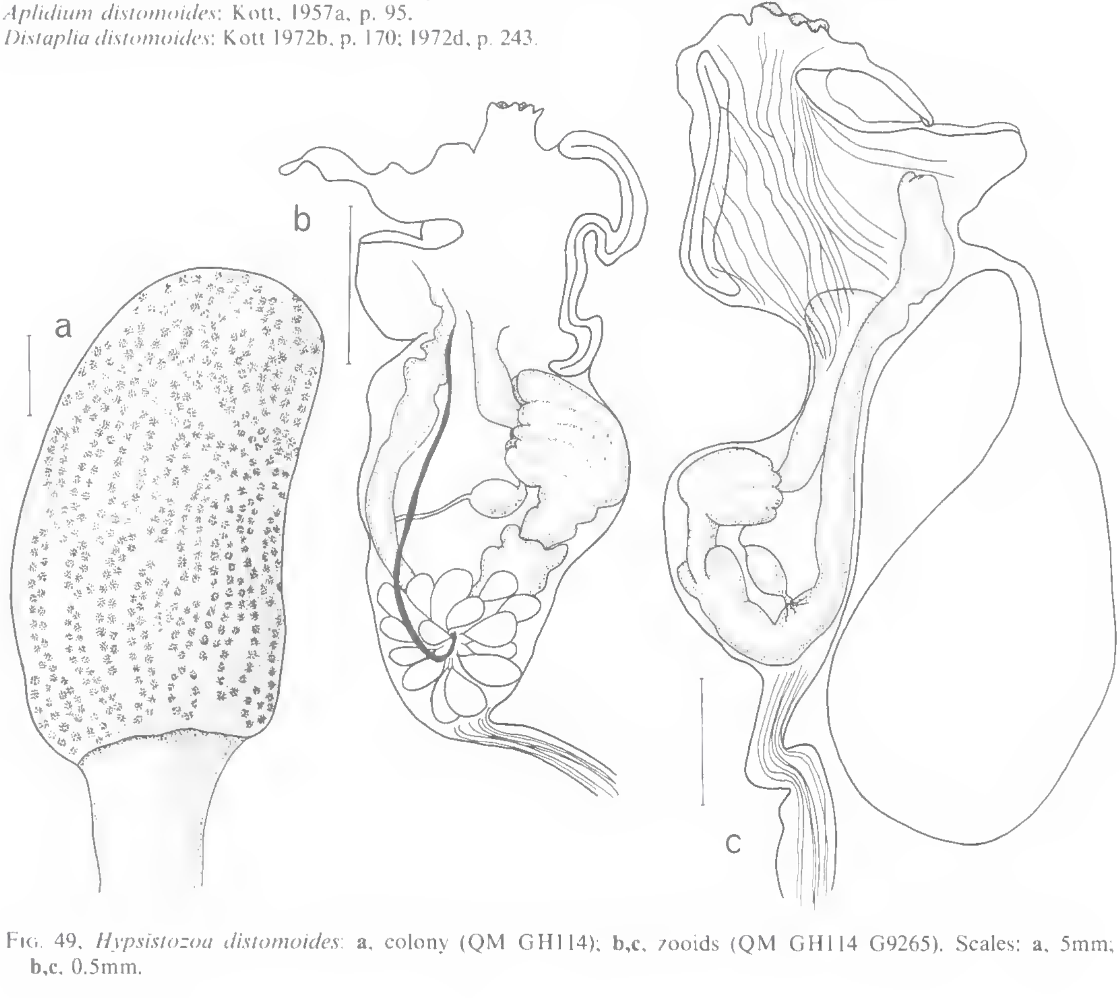


FIG. 49. *Hypsistozoa distomoides*: **a**, colony (QM GH114); **b**,**c**, zooids (QM GH114 G9265). Scales: **a**, 5mm; **b**,**c**, 0.5mm.

is only slightly translucent in preservative. Living colonies are reportedly rusty brown, orange, pink-purple or brilliant purple.

Internal Structure: Zooids are relatively small, the contracted thorax and abdomen (including the gonad) together being only 2mm long. The posterior abdominal vascular appendage is relatively wide with conspicuous muscle fibres extending along it. About 16 longitudinal and oblique muscles are on the thorax, the dorsal ones curving out into the large, rounded, anterior lip of the atrial aperture. Six small lobes are around the branchial aperture which is on a siphon with a well developed sphincter. There are 10 and 12 stigmata respectively in the posterior and 3 anterior rows on each side of the body. Each row is crossed by a parastigmatic vessel.

The oesophagus bends ventrally at right angles to its vertical proximal part to enter the stomach about one third of the way down the abdomen. The stomach is short and barrel-shaped with 8 distinct rounded folds that tend to flatten toward the pyloric end where the stomach tapers slightly to the mid-intestine. The mid-intestine is only short, opening directly into the rectum about two-thirds of the way down the abdomen. A distinct rectal valve is at the junction of the mid-intestine and the rectum. A large gastric reservoir is present in the loop of the gut — which is wide owing to the horizontal orientation of the stomach.

Heart and pericardium are in the posterior end of the abdomen to the left of the pole of the gut loop.

Gonads are in the top of the vascular process, just behind, and sometimes slightly overlapping, the right side of the pole of the gut loop. They consist of about 20 relatively short, pear-shaped follicles, their narrow ends projecting into the centre to join the vas deferens, which curves posteriorly and then dorsally before extending anteriorly to the atrial cavity. In zooids collected from Port Kembla in September and October one or 2 embryos are in a narrow-necked brood pouch attached to the dorsal border of the thorax just behind the atrial opening. In one colony (QM G9265) these embryos are tailed, and the trunks of the best developed are about 1mm long. They have an ocellus and an otolith in their cerebral vesicles, however no other organs can be seen. The narrow neck of the brood pouches is often long, the pouch projecting well behind the zooid into the centre of the colony. Colonies collected in March, April and May from South Australian localities contained maturing testes, but no developing embryos. The heart and pericardium are in the posterior end of the abdomen to the left of the pole of the gut loop.

Remarks: The species is distinguished from *H. tasmeriana* by the relatively few and wide stomach folds. Despite the fact that this species belongs to a different genus, its zooids resemble those of the South Australian species *Distaplia pallida* n.sp. in which the stomach has the same horizontal orientation, and similar, although more numerous, stomach folds.

Genus **Neodistoma** n.gen.

Type species: *Neodistoma mammillatum* n.sp.

This monotypic genus is characterised by its *Distaplia*-like zooids with a large atrial aperture and a lip from its upper border, parastigmatic vessels, a distinct rectal valve, a large gastric reservoir, and a conspicuous vascular process. The characters by which it is distinguished from *Distaplia* are its barrel-like (rather than kidney-shaped or oval) and distinctly folded stomach, and the 6 or more (rather than 4) rows of stigmata. There are no conspicuous muscles on the vascular appendage as there are in *Hypsistozoa*.

Most of the characters are common to all species of *Distaplia*, and the rectal valve is known in *D. stylifera*, *D. retinaculata* n.sp. and *D. prolifera* n.sp., and in *Hypsistozoa* spp. The presence of more than 4 rows of stigmata is unique in the Holozoidae. The genus is known only from South Australia.

Neodistoma mammillatum n.sp.
(Fig. 50. Plate 11a,b)

Distribution

Type Locality: South Australia (Seacliff, St Vincent Gulf, low limestone reef, on top of rocks, 12m, coll. N. Holmes 23.10.82, holotype SAM E1984 *QM GH4104*; Flinders I., Investigator Group, in caves, under rocks, 8m, coll. N. Holmes 10.4.83, paratype, QM GH2424.

Description

External Appearance: Colonies form wide, flat cushions, up to 4cm in diameter. The upper surface is uneven, with 3 to 5 or more shallow conical prominences up to 1cm high, each with a large terminal cloacal aperture. Zooids are in long double rows, one row each side of the canals that radiate from the terminal cloacal apertures. A mass of vascular processes from the zooids is in the central test of the colony. The test is soft and gelatinous. In preservative it is colourless and translucent. Living colonies are yellowish.

Internal Structure: Zooids are about 3mm long and crowded vertically in the test. The

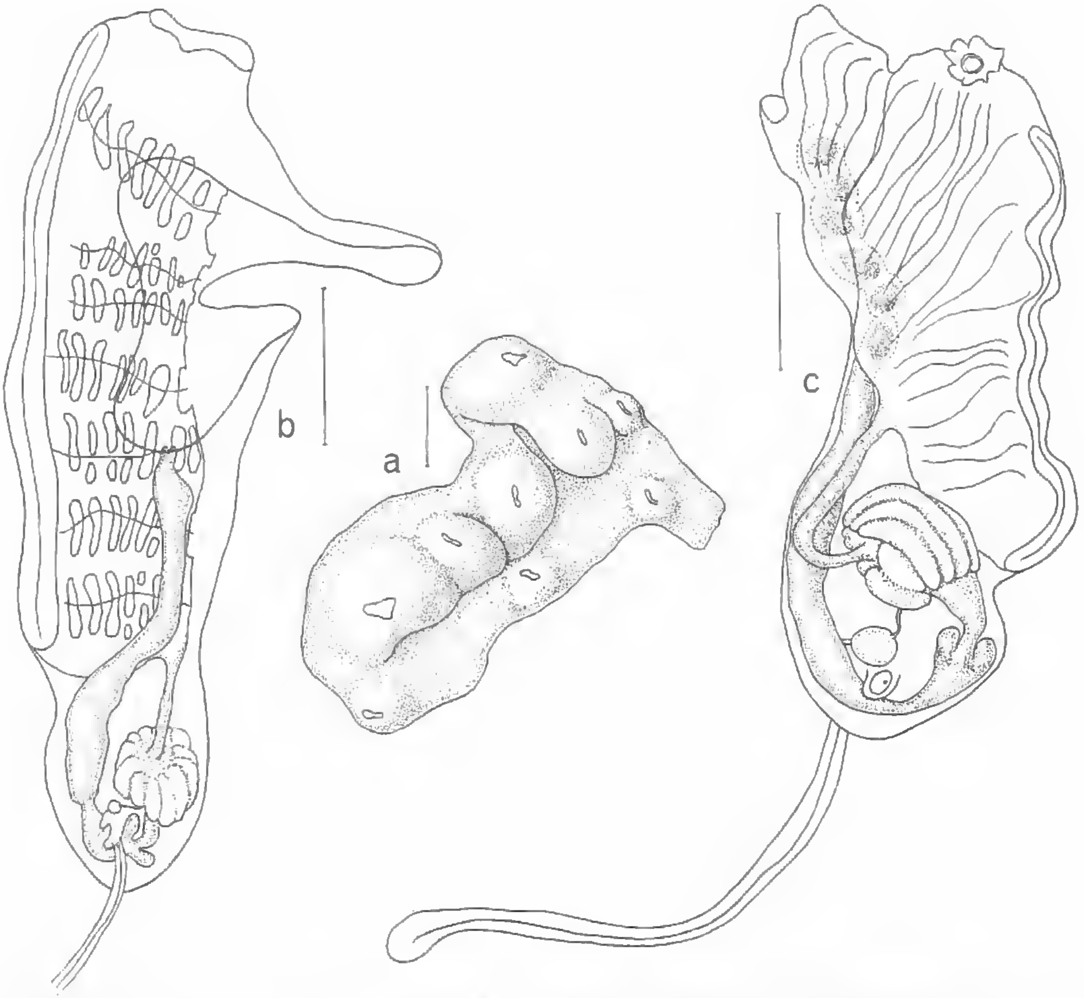


FIG. 50, *Neodistoma mammillatum* n.gen. n.sp.: **a**, colony (holotype SAM E1984); **b,c**, zooids (holotype SAM E1984, paratype QM GH2424). Scales: **a**, 5mm; **b,c**, 0.5mm.

branchial aperture has 6 wide lobes. The atrial aperture is a wide, asymmetrical opening, exposing the dorsal part of the branchial sac. Its asymmetry is related to the position of the zooid in relation to the cloacal canal. A large anterior lip projects from the upper border of the opening. About 20 fine longitudinal and oblique muscles are on the thorax, including dorsal muscles that extend out into the anterior atrial lip. The thorax is relatively long, with at least 6 rows each of 6 stigmata. The parastigmatic vessels bisect the stigmata in each row, to form additional rows. Following the horizontal division of each row of stigmata, new parastigmatic vessels develop across each of the new rows. Length of the stigmata varies greatly in each successive row. Small dorsal languets are on the parastigmatic vessels, alternating with the larger processes on the primary transverse vessels.

The abdomen is only about one-third of the length of the thorax. The oesophagus is narrow, and is either vertical, opening into a vertical stomach about halfway down the abdomen, or it is bent ventrally to open into a horizontally oriented stomach. The stomach is short, barrel-shaped, and has about 12 distinct, wide longitudinal folds. The mid-intestine is narrow, opening into the rectum at the posterior end of the descending limb of the gut loop. A conspicuous rectal valve is present. A large gastric reservoir is in the gut loop. Gonads are not mature in these specimens, and only occasionally is a small ovum found projecting from the body wall in the gut loop.

There always are numerous non-functional replicates scattered amongst the functional adult zooids.

REMARKS: In addition to the unusually large number of rows of stigmata, this species can be distinguished by its well-formed stomach folds and the small number of stigmata in each row. Additional sampling is needed to acquire specimens in which gonads and larvae are mature.

Genus **Sycozoa** Lesson, 1830

Type species: *Sycozoa sigillinoides* Lesson, 1830

The genus is characterised by its regular, highly organised and always stalked colonies in which the zooids are in double rows along each side of vertical cloacal canals that extend, parallel to one another, down the sides of the head of the colony. The stalk is sometimes short, thick and fleshy as in *Distaplia*, but in several species of *Sycozoa* the stalk is long, thin, hard and leathery. Lobes around the branchial apertures are reduced and usually absent altogether. The body musculature is reduced. Apart from some fine bands around each aperture, the body wall has only a few (not more than 5) fine muscles on the thorax, none on the abdomen. Parastigmatic vessels are never present, and the 4 rows of stigmata are in two pairs in which the adjacent ends of the stigmata of each pair-partner line up along each side of the transverse vessel that separates them. At their opposite ends the stigmata progressively reduce in length toward the endostyle, leaving a large triangle of unperforated pharyngeal wall between the ventral ends of the second and third rows of stigmata. There is also an area of unperforated pharyngeal wall both anterior and posterior to the perforated section. The atrial cavity extends only over the stigmata, not over the unperforated parts of the pharyngeal wall consequently the ventral part of the cavity is separated into two pouches by the triangular area between the ventral ends of the second and third rows of stigmata. The stomach is smooth walled and pear-shaped. It opens into a short duodenal area that is only slightly smaller in diameter than the distal part of the gut, with which it forms a smooth cylindrical tube without subdivisions. A small gastric reservoir is present in *S. cerebriformis* and occasionally in *S. sigillinoides*, but not in other species. Gonads are either in the gut loop, or spill out behind it, or are contained in a sac protruding from the side of or behind the abdomen but never much constricted from it. A brood pouch from the postero-dorsal corner of the thorax sometimes is long and curved at its distal end. It contains up to 40 developing embryos, the largest numbers being in Antarctic species. Variable numbers of embryos are brooded. Usually colonies are dioecious and all the heads of a compound colony are of the one sex. However, with apparently long periods when gonads are not developed, it is not known whether a colony remains the same sex throughout its life. Only in one species are there male and female zooids present at the same time in one colony (*S. anomala* Millar, 1960). Larvae are released from the top of the progressively disintegrating head of the parent colony, which sometimes, detached from its stalk, forms a large floating brood sac.

Replication from isolated vegetative stolons in the stalk of the colony is prolific, zooids being added to the systems at the top of the stalk. Stalks persist after disintegration of the heads and new heads develop from the vegetative material stored in the stalk (Caullery 1909; Salfi 1925a, 1926; Millar 1960).

Larvae of *Sycozoa* have a large trunk, well developed adult organs, and triradially arranged adhesive organs, 2 dorsal and one ventral, each with a large axial cone set in a deep epidermal cup at the end of a smooth elliptical stalk. The hyaline cap on the axial cone is often large. There are no ectodermal ampullae and no frontal plate. The ectoderm and test of the stalk of the adhesive organs appears specialised in some species (see *S. pulchra*, *S. brevicauda* n.sp.) and may have secretory cells and be adhesive. The ocellus is absent. Larval budding in *Sycozoa*, as in *Distaplia*, is never as prolific as it is in *Hypsistozoa*, nor do the buds develop to blastozooids as they do in the latter genus. However in some species of *Sycozoa* (*S. pulchra* and *S. brevicauda* n. sp.), the vegetative stolon (the left epicardial sac) is long and conspicuous and persists in the larval trunk after the buds have formed.

The form of the systems does vary. Usually each long canal has a single opening, the openings arranged around the margin of the free end of the head. There they open either directly to the exterior, or into a terminal cloacal cavity with a central apical opening. Unlike *Distaplia* the rows of zooids never converge onto the upper surface of the head. In a few species canals expand into the centre of the head, becoming confluent with one another, and creating a large internal cavity that opens by a single terminal aperture as in *Cyathocormus* Oka, 1912. The latter genus was erected to accommodate a species (*C. mirabilis*) in which the double rows of zooids typical of *Sycozoa* are embedded in the cylindrical walls of a stalked, cup-shaped colony and project into the central cavity in parallel longitudinal ridges of test. The atrial apertures open directly into the central cavity in the long furrows between the double rows

TABLE 6. Summary of Characters of the Species of *Sycozoa* Recorded from Australia

Species	[1]Biogeographic description	[2]Range around Australia	Zooid-bearing part of colony	Stalk	Stigmata (per row)	Testis follicles (number)	Larval trunk (length, mm)	Other
S. cerebriformis	A,te	Shark Bay–Port Stephens	flat, pleated continuous lamellae	short, thick fleshy	13–14	4–5	0.8–1.1	gastric reservoir present; one embryo per brood pouch
S. seiziwadai	WP,tr	NSW Cape Jaubert	flat, fan-shaped lamellae fusing with one another	″	12–14	6	0.6	one embryo per brood pouch
S. murrayi	A,te	SA–NSW	flat, paddle-shaped	short, narrow firm	12–14	5	0.7	test firm, dark
S. brevicauda n.sp.	A,te	Port Hedland–SA	flat, fan-shaped	long, narrow firm	10–12	9	0.6	root-like hairs at base of stalk
S. pulchra	A,tr-te	Dongara–Torres St	inverted cone-shaped	″	14–16	6	1.5	root-like hairs at base of stalk; papilla on abdominal wall
S. pedunculata	A,te	King George Snd–NE Tasmania	inverted cone shaped	long, narrow leathery	14-20	8–10	0.9	—
S. sigillinoides	PSP	SA, Tas.	conical, terminal cloacal aperture	″	16–26	12–18	0.4–0.76	cloacal canals and terminal chamber; terminal cloacal aperture
S. cavernosa n.sp.	A,tr	Dampier Arch. Cockburn Snd	conical, terminal cloacal aperture	short, thick fleshy	10–12	5	?	central cloacal chamber; terminal cloacal aperture; posterior abdomen present

[1]A, Indigenous; P, Antarctic; SP, Subantarctic; tr, tropical; te, temperate. [2]Range given anticlockwise around the continent.

of zooids. *Sycozoa cavernosa* n. sp. from Western Australia has such a cloacal system. In smaller colonies the head is cup shaped as in the Japanese species. In larger colonies the upper third of the head has an identical open cloacal cavity, although in the middle third of the head there is a central core of test connected to the outer zooid-bearing layer by horizontal radial test connectives. The lower part of the head, where new replicates are being added to the system, is solid. Further up, the backward expansion of the cloacal cavity tends to partially separate the central test from the outer zooid-bearing layer. This elaboration of the cloacal cavity does not justify the separation of the genus *Cyathocormus* from *Sycozoa*, and the genera are treated here as synonyms.

The homologue of the large internal cloacal cavity of *S. cavernosa* can be observed in some specimens of *S. sigillinoides* when the terminal cloacal cavity enlarges as the top of the head begins to disintegrate (releasing its larvae). The atrial openings of the zooids are thus exposed directly to the central cavity.

In species with separate openings of cloacal canals around the margin of the upper surface of the head, disintegration of the terminal central test sometimes leaves a concavity that can be mistaken for a cloacal cavity with a wide terminal opening.

Difficulties in interpreting the exact location of cloacal apertures that arise from the disintegration of the top of the head were observed by Michaelsen (1924), and Millar (1960). Their location is also obscured by the fact that they become large, extending down the sides of the colony in a deep V, and exposing the cloacal canals with the atrial apertures of the zooids directly to the exterior.

Since headless stalks persist, and the isolated vegetative stolons contained in them subsequently produce new zooids and regenerate new heads, the colonies are probably long-lived. Much of the variability observed probably is caused by growth, this being rapid resulting from prolific replication of zooids. The presence of numbers of heads from a single base probably results from growth following regression of a single head (Millar 1960) and is not necessarily indicative of a genetic difference from individuals with single heads and unbranched stalks. There is little intraspecific variation either in the numbers of stigmata in each row, or in the shape and texture of the head and the stalk, or in the numbers of testis follicles. Thus it is these characters that must be used to distinguish the species, for the shape of the stomach, the condition of its wall and the course of the gut are all remarkably constant throughout the genus.

The genus is relatively diverse in Australian waters where 8 of the 14 known species have been recorded. The Australian records comprise 5 indigenous species, two tropical West Pacific species (*S. seiziwadai* and *S. pulchra*) and one Antarctic species (*S. sigillinoides*).

The Antarctic members of the genus have wide geographic ranges. Their larvae lack an ocellus that would attract them into shaded settlement sets, and in any case shaded places seldom occur in their open sea floor habitats. Accordingly, their settlement sites are not restricted, and this may contribute to gene flow (Berrill 1955). The genus appears to have Antarctic affinities. *Sycozoa kanzasi* from Japan, is the only species that extends north of the tropical western Pacific; and although the two known Antarctic species, *S. sigillinoides* and *S. georgiana* (see Millar 1960, and Kott 1969) have a wide circumpolar range in the Southern Ocean, the genus has not otherwise been recorded from the Atlantic Ocean. The western Pacific tropical species and Australian temperate species have clear affinities with the fauna of the Southern Ocean, *viz. S. seiziwadai* with the South African *S. arborescens*, and *S. pulchra*, *S. pedunculata* and *S. brevicauda* n.sp. with *S. sigillinoides*. The Australian continent appears to have served as a bridge between Antarctic and tropical waters for radiation of this genus.

KEY TO SPECIES OF THE GENUS *SYCOZOA* RECORDED FROM AUSTRALIA

1. Cloacal aperture single, in centre of free end of head 2
   Cloacal apertures numerous around outer margin of free end of head 3
2. Zooids embedded in longitudinal ridges projecting into a central cloacal cavity, gonads posterior to the gut loop .... *Sycozoa cavernosa* n. sp.
   Zooids not embedded in longitudinal ridges projecting into central cloacal cavity; gonads at the side of the gut loop .... *Sycozoa sigillinoides*
3. Base of stalk with root-like hairs 4
   Base of stalk without root-like hairs 5
4. Papilla present on body wall over pyloric end of stomach .... *Sycozoa pulchra*
   Papilla not present on body wall over pyloric end of stomach . . *Sycozoa brevicauda* n.sp.
5. Zooid bearing part of colony pleated .... *Sycozoa cerebriformis*
   Zooid bearing part of colony not pleated . . . 6

6. Stalk thin and leathery, and very much longer than head .... *Sycozoa pedunculata*
   Stalk not thin and leathery, and not very much longer than head 7
7. Stalks branch; test not firm and darkly pigmented .... *Sycozoa seiziwadai*
   Stalks do not branch; test firm and darkly pigmented .... *Sycozoa murrayi*

The species known from adjacent areas are:

Sycozoa anomala Millar, 1960 (see also Millar 1982) from New Zealand has its gonads in a posterior abdominal sac (as in *S. cavernosa* n.sp.), a terminal common cloaca, narrow rather than fleshy stalks, small branchial lobes and occasionally hermaphroditic colonies.

Sycozoa arborescens Hartmeyer, 1912 from South Africa has colonies with fleshy branching stalks that resemble those of *S. seiziwadai* (see Michaelsen 1923, Millar 1963a). However each zooid-bearing head has a terminal cloacal cavity with a central aperture rather than separate openings around the head.

Sycozoa gaimardi (Herdman, 1886), known only from the Magellanic region (see Kott 1969) has dome-shaped heads on slender stalks.

Sycozoa georgiana (Michaelsen, 1907) a circumpolar Antarctic species has a more restricted range than *S. sigillinoides*, not extending north of the Antarctic convergence. Its main characteristic is the short zooid rows resembling those of some specimens of *S. seiziwadae*, however it has the single cloacal aperture and narrow stalk of *S. sigillinoides*.

Sycozoa kanzasi (Oka, 1930) from Sagami Bay, Japan, resembles *S. pulchra* in the presence of a knob over the stomach, a narrow stalk and basal roots. It is distinguished by its single terminal cloacal aperture (Tokioka 1953, Millar 1975)

Sycozoa mirabilis (Oka, 1912) from Sagami Bay is distinguished from *S. cavernosa* n. sp. by its cup-shaped rather than cone-shaped colony, fewer zooids per vertical row, and the much shorter and fleshier stalk supporting the zooid bearing head.

Sycozoa brevicauda n.sp.
(Fig. 51)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Cockburn Sound, coll. Western Australian Naturalist 28.5.58, holotype WAM 139.75; off Eglinton Rocks, on floor of cave at about 45m, coll. P. Roberts 22.12.75, paratypes WAM 801.83; 71 nautical miles N. of Port Hedland, 81–2m on sand, coll. L. Marsh and M. Begant, paratype WAM 1046.83).

FURTHER RECORDS: Western Australian (Steep Point, QM GH4364; Houtman's Abrolhos, WAM 804–5.83). South Australia (Grange, SAM E2011).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of a flattened, fan-shaped head up to 3cm wide at the widest point. The head is supported on a long (up to 8cm) narrow stalk, sometimes several arising from a common basal stalk that, tuber-like, runs along the surface of the substrate. The stalk is relatively hard, with a tough outer cuticle. Zooids are in vertical double rows that radiate out along the fan-shaped head. The lower half of the fan contains non-functional vegetative zooids from the vegetative stolons in the stalk being added to the double-row systems. The upper, wide part of the fan contains rows of up to 20 functional zooids. The long cloacal canals between the double rows of zooids open around the zooid-free, flat, narrow, arched terminal surface of the head. The stalk narrows toward its base where it terminates in a clump of hair-like roots that have a mass of sand entangled in them. Sometimes (apparently wherever it touches the substrate) clumps of roots along the length of the stalk provide supplementary points of attachment.

INTERNAL STRUCTURE: Zooids are about 2mm long, the thorax and abdomen of about equal length. Branchial lobes are absent and the atrial aperture is the usual wide opening into the cloacal canal. It is asymmetrical, the shape of the opening dependent on the side of the cloacal canal on which it is located. The branchial sac has 12 stigmata in the anterior pair of rows and 10 in the posterior rows. The stomach is comma-shaped, tapering to the intestine. The intestine and rectum together form a continuous cylindrical tube without any divisions in it. The stomach is slightly obliquely oriented. Gonads are contained in the gut loop, projecting from the posterior end of the loop when mature. Colonies are dioecious. Up to 9 long male follicles lying parallel to one another in a barrel-shaped clump are in a zooid from a male colony. The vas deferens curves posteriorly from the outer end of the clump of follicles before extending anteriorly with the rectum.

Brood pouches containing an embryo and one egg in the upper part of the head of specimens collected from Port Hedland in October (WAM 1046.83) and in the holotype specimen collected in May.

Larvae are relatively small, the trunk only 0.6mm long, with the tail barely reaching its anterior end. There is an otolith but no ocellus.

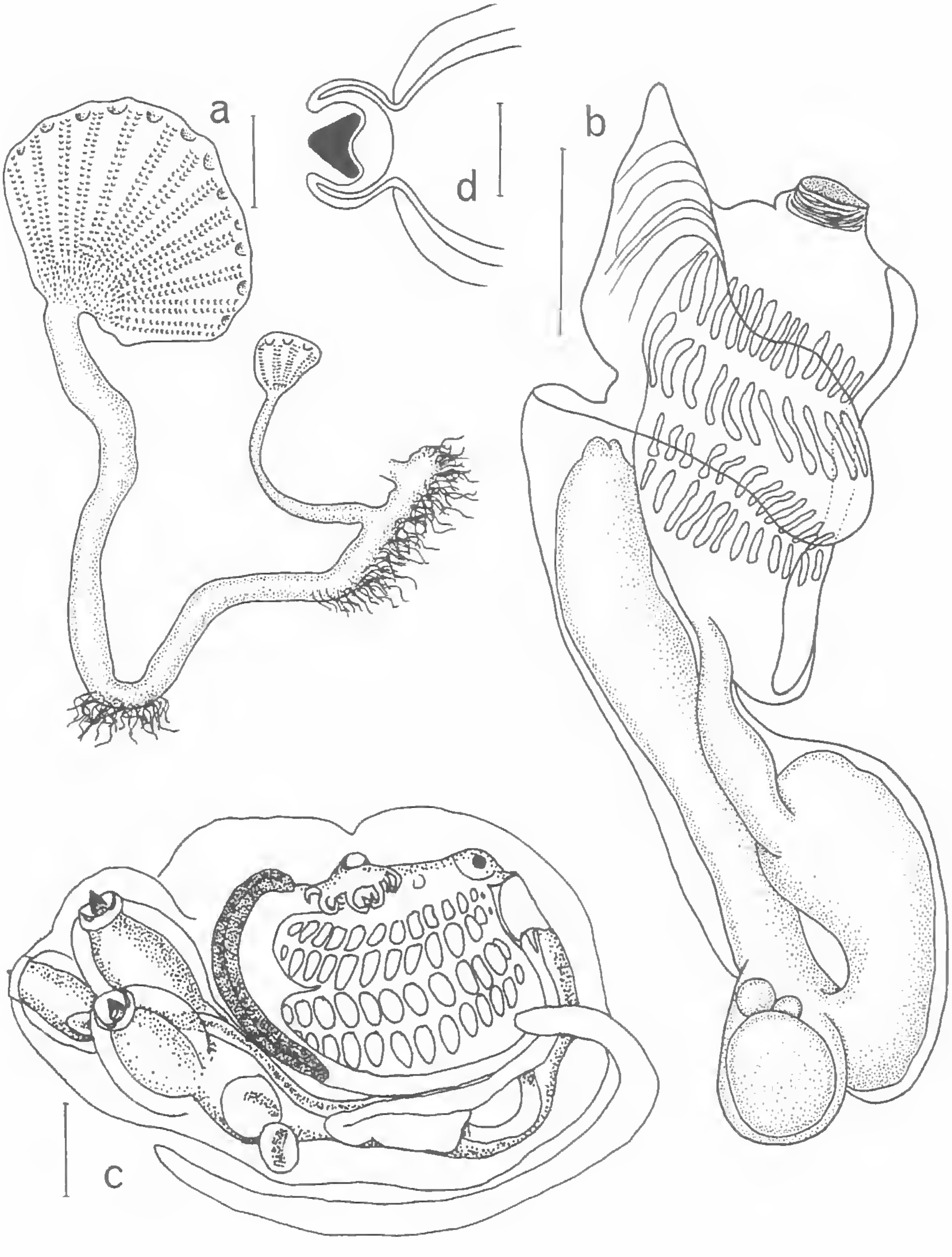


FIG. 51, *Sycozoa brevicauda* n.sp.: **a**, colony (holotype WAM 139.75); **b**, zooid (holotype WAM 139.75); **c**, larva (paratype WAM 1046.83); **d**, adhesive organ showing hyaline cap in ectodermal cup (paratype WAM 1046.83). Scales: **a**, 1cm; **b**, 0.5mm; **c**, 0.1mm; **d**, 0.05mm.

The left epicardial sac is long, narrow, and persists, projecting anteriorly from the left side of the gut loop to lie between the thick elliptical stalks of the 3 triradially arranged adhesive organs. These stalks diverge from one another and project from the anterior end of the trunk, each surrounded by a layer of test. Ectodermal cells of the stalks have fine cilia-like extension through the test, and these form terminal expansions at the surface.

REMARKS: The species resembles *S. pulchra* in the presence of a long, narrow stalk with clumps of hair-like roots fixing to the sandy substrate. However, the head of the present species is wide and flat, the head of *S. pulchra* being cylindrical in section and more like an inverted cone. There are slightly fewer stigmata per row, and 9 (rather than 6) male follicles in the present species. The projection from the body wall over the pyloric end of the stomach, characteristic of *S. pulchra*, does not occur in the present species. Larvae are also similar, with a long epicardial tube, deep adhesive organs, and unusual ectodermal cells on their stalks. However the larval trunk of the present species is about half the length of that of *S. pulchra*.

Sycozoa cavernosa n.sp.
(Fig. 52)

DISTRIBUTION

TYPE LOCALITY: Western Australia (off Whitford Beach, Cockburn Sound, reef 5m, coll. L. Marsh 16.2.79, holotype WAM 795.83 *QM GH2106*; off Whitford Beach, 3 4m, coll. L. Marsh 16.11.79, paratypes WAM 879.83; Woodmans Point, Cockburn Sound, coll. A. Brearley 31.12.74, paratype WAM 199.75).

FURTHER RECORDS: Western Australia (Dampier Archipelago, WAM 1000.83; Cockburn Sound, WAM 219 20.73 805.83 807.83, QM G9653).

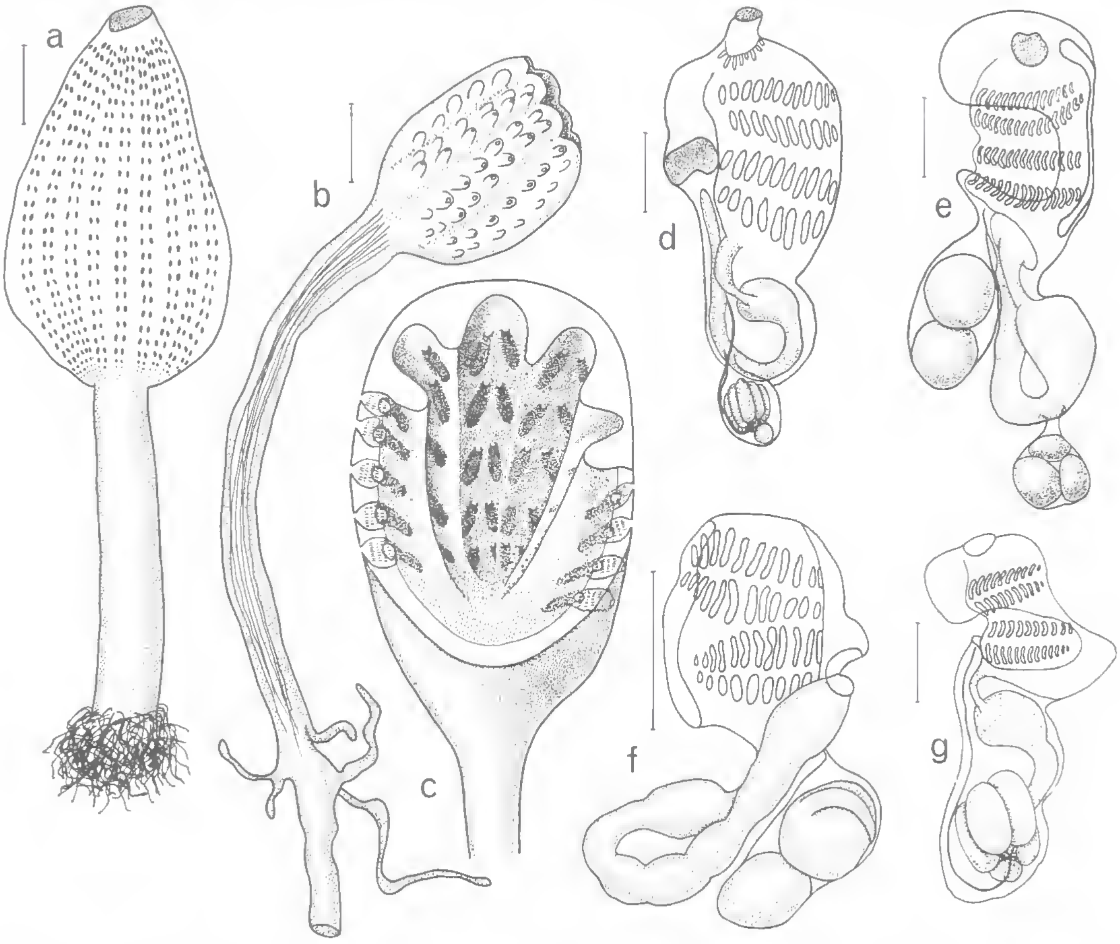


FIG. 52. *Sycozoa cavernosa* n.sp.: **a**, mature colony (holotype WAM 795.83); **b**, young colony (WAM 1000.83); **c**, diagram of interior of the head; **d**, juvenile zooid with precocious gonads (paratype WAM 879.83); **e**,**f**, female zooids (paratype WAM 199.75 1000.83); **g**, male zooid (holotype WAM 795.83). Scales: **a**, 1cm; **b**, 2mm; **d**, 1mm; **e**,**f**, 0.5mm.

The species has been taken down to 18 m. It has not been taken outside Cockburn Sound.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are conical, pointed heads up to 7cm long and 3cm diameter at their base, on more or less cylindrical stalks about 1cm in diameter narrowing slightly toward the base usually about the same length as the head, but occasionally longer. Basally each stalk breaks into short hair-like projections which, when entangled with sand, create a small and more or less spherical holdfast. A large cloacal cavity in the top of the head has a large terminal opening. Zooids are in the outer layer of test, arranged in double rows extending down the sides of the head of the colony. Double rows of zooids are embedded in longitudinal ridges of test that project into the internal cavity. In the lower part of the head the terminal cavity continues down separating the outer zooid-bearing test from a central core continuous with the stalk. The outer zooid-bearing layer is joined to the central core by radial connectives, which are strands of test about 3mm in diameter that extend horizontally from the central test core and cross the cloacal cavity to join the zooid-bearing ridges of test. Vascular appendages of the zooids extend through these connectives, into the inner core and thus down into the stalk. Atrial apertures of zooids open directly into the cloacal cavity between the projecting zooid-bearing longitudinal ridges. Capacious cloacal spaces in the heads of mature colonies cause heads to be flaccid in preservative. Colonies in which vegetatively produced zooids are maturing have less extensive cloacal spaces and are firmer, while in one small colony the centre of the head is an open cloacal space without any central test core (WAM 1000.83). The colour of living colonies is not known. In preservative they are beige with grey zooids.

INTERNAL STRUCTURE. Zooids orient obliquely in the colony with their atrial apertures uppermost (opening into the adjacent cloacal canal), with their abdomina and posterior abdominal sacs projecting into the radial test connectives. Thorax and abdomen together are up to 2mm long. The posterior abdominal sac is about half that length only when the male gonad is mature. The small branchial aperture is not lobed. The atrial aperture is large, the sides of the aperture being drawn back to expose most of the branchial sac to the cloacal cavity. The upper border of the opening is produced into a rounded lip. Fine muscle bands are in the thoracic body wall, but are inconspicuous and not numerous. There are 12 long rectangular stigmata in the 2 anterior rows and 10 in the 2 posterior rows.

The pear-shaped, smooth-walled stomach, tapering to its pyloric end, is halfway down the abdomen. No other divisions of the gut were observed.

Gonads occupy the narrow-necked sac behind the abdomen. Male and female gonads are never present together, and all the zooids in the colony are of one sex. Mature testis follicles (5) are in paratype material collected in November (WAM 879.83). Mature ova (3 to 5) are in a colony collected in December (WAM 199.75) and in this colony up to 3 early embryos are in a long brood pouch with a short, narrow neck connecting it to the postero-dorsal corner of the thorax. Colonies collected in September (WAM 219–20.73) have only immature zooids, an incipient posterior abdomen without contained gonads being present, and in these colonies the cloacal cavities are more limited. In colonies taken in June (WAM 805.83, 807.83) the head is relatively firm, there are no gonads, only a few cloacal spaces and no cloacal aperture, and the zooids are juveniles, embedded in the test.

Apparently sexual reproduction occurs at the beginning of summer (December) and larvae may be released in January and February. Thereafter the zooids may regress, vegetative zooids reappearing in June, developing through late winter and spring (August to November). Larvae of this species are not known.

REMARKS. The extensive internal cloacal cavity with longitudinal ridges (containing embedded zooids) projecting into it, and the wide terminal aperture, together with the smooth outer surface of the colony readily distinguish it. The head of the juvenile specimen (WAM 1000.83) resembles *S. mirabilis* (Oka, 1912) although Oka's specimens were larger with a short fleshy stalk and appear not to be conspecific with the present species. Gonads were not developed in *S. mirabilis*. Their presence in a posterior abdominal sac in the present species, as in some species of *Distaplia*, resembles *Sycozoa anomala* Millar, 1960, however Millar's species (from New Zealand), does not have the open cloacal cavity of the present one.

Sycozoa cerebriformis (Quoy and Gaimard, 1834)
(Fig. 53, Plate 11c–h)

Aplidie cerebriforme Quoy and Gaimard, 1834, p. 62.
Sycozoa cerebriformis: Brewin, 1953, p. 58. Kott, 1957a, p. 99; 1972a, p. 8; 1972b, p. 170; 1976, p. 57. Millar 1963a, p. 708; 1966a, p. 365.
Distaplia cerebriforme: Michaelsen, 1924, p. 325.
Colella plicata Herdman 1899, p. 62.
Colella incerta Caullery, 1909, p. 10.

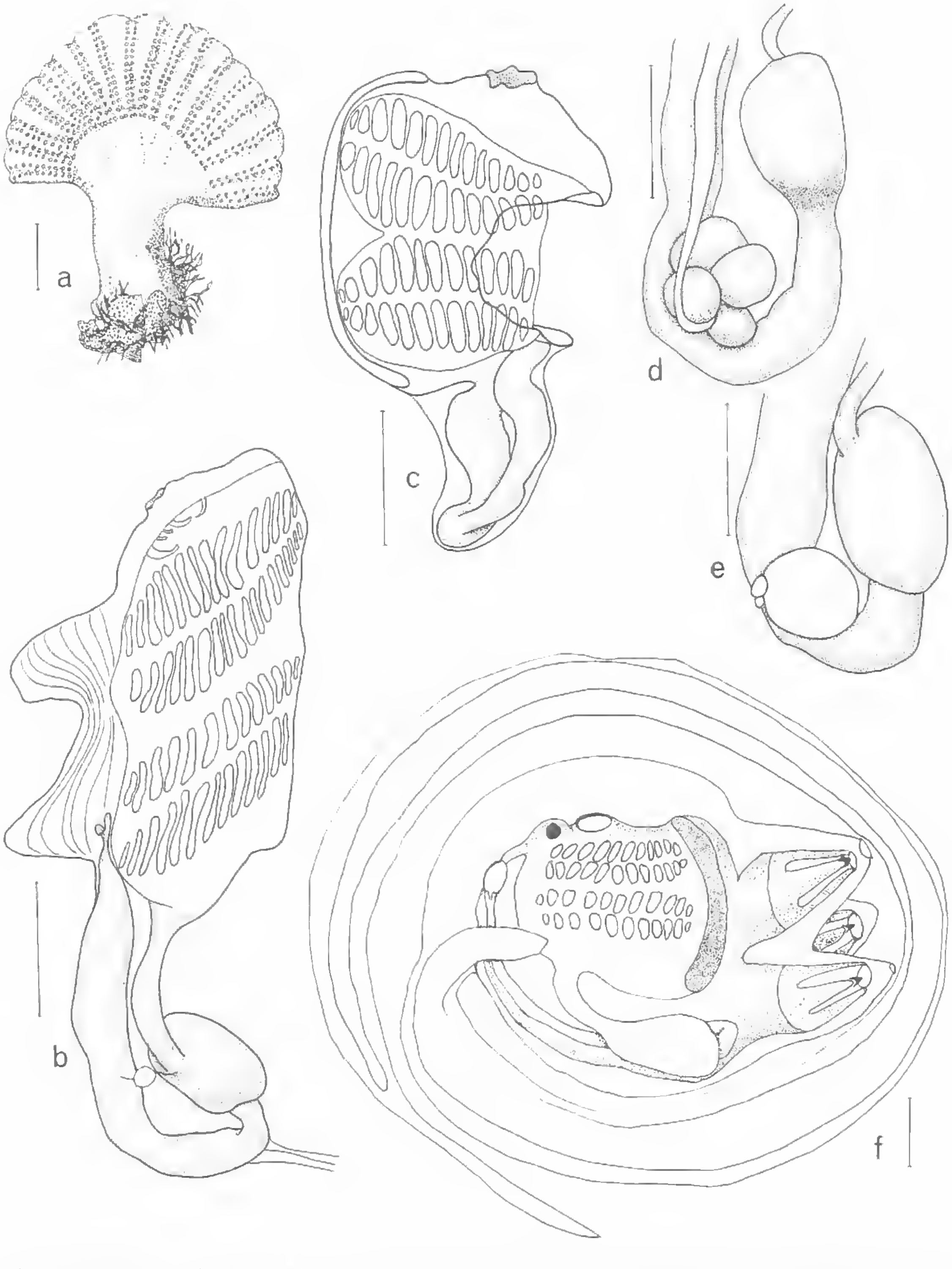


FIG. 53, *Sycozoa cerebriformis*: a, young colony (QM G9637); b, zooid (SAM E2020); c, juvenile vegetative zooid (SAM E2013); d,e, abdomens of male and female zooids (SAM E2021); f, larva (QM GH2405). Scales: a, 1cm; b–e, 0.5mm; f, 0.1mm.

DISTRIBUTION

NEW RECORDS: Western Australia (Shark Bay, WAM 797.83; Houtman's Abrolhos, WAM 805–6.83; Dongara, WAM 1047–9.83; Cockburn Sound, WAM 159.74 21.75 24.75 87.75 94.75 131.75 209.75 219.82 798–800.83 1043–4.83). South Australia (Great Australian Bight, SAM E2001 E2011 E2014–5 E2021; Nuyts Archipelago, SAM E2019–20 E2030, QM GH4214; Spencer Gulf, SAM E2012 E2017 E2022–3 E2025–9 E2045; St Vincent Gulf, SAM E1954-6 E1958 E2018 E2024, QM GH2405 GH4224; West I., SAM E2013, QM G9264 GH2405). Victoria (Gabo I., SAM E2016, AM Y2137; Bass Strait, QM G12735 GH2393–4, MV H462 H475 H929). Tasmania (Swansea, TM D93 D191; Port Davey QM GH1844). New South Wales (Bateman's Bay, AM Y2147; Jervis Bay, QM G10015-6; Port Kembla, QM G9262; Port Stephens, AM Y2135; Monavale AM Y2136; Port Jackson, AM Y2188; Nambucca Heads QM G10009; Solitary I. QM G9637; Cook I., QM GH4223). Queensland (Mooloolabah, QM G10107).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — QM G9263 Kott 1972b; St Vincent Gulf — Kott 1957a, SAM D268, QM G9317 Kott 1972a; West I., Wright I. — Kott (1972a). Victoria (Western Port, Port Phillip Bay — Quoy and Gaimard 1834, Caullery 1909, Kott 1957a 1976, Millar 1963a 1966a). New South Wales (Jervis Bay, Port Hacking, Port Jackson, Port Stephens — Herdman 1899, Kott 1957a, Millar 1963a).

The colonies from Dongara and Shark Bay (WA) are all small and these may represent populations at the northern extremity of the range of this temperate indigenous species. The species is taken in caves and crevices off reefs, and dredged off the sea floor at depths down to 50m.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of a relatively short (usually not more than 1.5cm long) fleshy (up to 3cm in diameter) stalk that flattens out at the top where it expands into a flat, ribbon-like, zooid-bearing lamella up to 2cm high. Occasionally the stalk is longer (up to 7cm) and cylindrical. The top edge of the zooid-bearing lamella is flat and zooid-free. In young colonies the lamella is merely flat and spade-shaped, but as the colony develops it increases in width. At first it curves around at each end, its junction with the top of the head being horse-shoe shaped. Subsequently it becomes long and is gathered and pleated onto the top of the stalk. One colony (SAM D268) has a lamella that is 74cm wide, gathered onto the top of a stalk of about 3cm diameter to make a complex rosette 8cm in diameter. Sometimes the basal stalks branch, each terminal branch having an expanded zooid-bearing part that usually fuses with that of its neighbour. A thin layer of test sometimes connects the branches of adjacent stalks.

Zooids are in parallel double-row systems down each side of the flat lamellae. Each cloacal canal opens by a separate large aperture at the top of the canal, the apertures are around the margin of the flat, narrow upper surface of the lamella. The double row systems seldom contain more than 8 functional zooids in each row. These occupy a band about 1cm wide along the upper part of each side. The lower 1cm has a band of non-functional replicates progressively joining the vertical rows of functional zooids, and, lower down, just above the stalk, the basal stolons of the adult zooids converge into the stalk. The surface test is covered with minute, evenly spaced inconspicuous pointed papillae.

In life, specimens of this species with their tightly pleated rosette-like colonies are spectacular. A range of colours is known. Collector's notes for colonies taken from 25m off Mooloolaba (QM G10107) indicate they were yellow, but changed to purple when damaged or removed from the substrate. Specimens photographed in *situ* are blue, pink, red, orange, or yellow. In preservative they are sometimes translucent blue, pink or cream.

INTERNAL STRUCTURE: Mature zooids are up to 2.5mm long, delicate, with thoraces collapsed in preserved material, but never contracted. Muscles are around the apertures, but only about 5 fine muscles extend from the branchial siphon a short distance down each side of the pharynx. There are 14 stigmata in the anterior pair of rows and 13 in the posterior rows. The oesophagus is fairly long, the small oval stomach slightly oblique, the gut loop almost vertical, and a small spherical gastric reservoir is in the gut loop.

Colonies are dioecious. Gonads are on the right side of the gut loop. The ovary contains up to 3 ova, and the testis 4 or 5 wedge-shaped follicles arranged in a tight circle. Short vasa efferentia from each follicle join the vas deferens in the centre of the circle. The vas deferens then makes a short loop posteriorly before extending anteriorly along the inside of the rectum.

The breeding season for this species appears short. Colonies collected from South Australia had mature male and female gonads in May (SAM E2021). Embryos are in one colony taken in April (SAM E2014) and one in May (QM GH2405). Although gonads are sometimes present in March, July and October, they are not mature. Gonads were not present in any of the specimens collected in January or February. Material was collected from western Australian waters in all months except January and February. Most sexually mature colonies were males taken from October to December (WAM 94.75 802.83 131.75 798.83), although one mature male colony was taken in May. One colony with larvae and embryos was taken from Cockburn Sound in December (WAM 799.83). In general, the species reproduces sexually in spring and autumn. The significance of the preponderance of male colonies present in the collections is not understood.

In this species there is only one almost spherical embryo in each brood pouch. The larval trunk is 0.8 to 1.1mm long and the tail is wound one and a half times around it. There is an otolith but no ocellus, and neither epicardial tube nor buds have been detected. The adhesive organs are large with tall, narrow axial cones and epidermal cups, and short, thick stalks. Each adhesive organ protrudes from the anterior end of the trunk surrounded by a layer of test.

REMARKS: The flat, ribbon-like, pleated, zooid-bearing part of the colony, together with the short systems containing less than 10 functional zooids per row are distinctive characters. Further this is the only species of the genus in which a gastric reservoir is always present, though *S. sigillinoides* sometimes has one (Kott 1969).

Sycozoa brevicauda n. sp., which also has a flattened head, does not have the short rows of zooids nor the ribbon-shaped head of the present species (its head being fan-shaped); nor does it have the short fleshy stalk of the present species.

The species appears related most closely to the tropical *S. seiziwadai*, which it resembles in having branched fleshy stalks, short systems, relatively few male follicles, a single larva in each brood pouch, large larval adhesive cones and no conspicuous epicardial tube extending to the front of the larval trunk. *Sycozoa seiziwadai* is distinguished from the present species by its narrower zooid-bearing heads that are not pleated, a longer and narrower gut loop, the absence of a gastric reservoir, and a smaller larva with a shorter tail and larval buds.

Sycozoa murrayi (Herdman, 1886)

(Fig. 54. Plate 12a)

Colella murrayi Herdman, 1886, p. 115, var. rubida p. 119.

Sycozoa murrayi: Kott, 1957a, p. 97.

Sycozoa tasmanoides Kott, 1954, p. 157.

DISTRIBUTION

NEW RECORDS: South Australia (Great Australian Bight, QM GH4155; St. Vincent Gulf, QM GH4220). Tasmania (Midway Point — TM D1187; northeastern Tasmania, TM D1835).

PREVIOUSLY RECORDED: Tasmania (off Maria I. AM Y1231 Kott 1954). Victoria (Bass Strait — Herdman 1886). New South Wales (off Port Jackson — var. rubida Herdman 1886; Bermagui — Kott 1957a).

The species appears indigenous and temperate, ranging from the Great Australian Bight to the vicinity of Port Jackson.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies have a flattened and paddle-shaped, or a smooth oval, stalked head. The newly recorded specimens have heads 2cm long, about 1cm wide across the middle or widest part and only about 0.5cm thick. Posteriorly the head tapers to the narrow firm, short stalk that is never more than slightly longer than the head and lacks an outer hard cuticle. The stalk narrows toward the base and terminates in a rather blunt point without breaking into either roots or hairs. The lower part of the stalk adheres, along its length, to the sustrate (weed stems, fronds). In specimens recorded by Herdman (1886) and Kott (1957a) the stalk is shorter and thicker.

The test is unusually firm, containing bluish-black pigment particles present also in the body wall of the zooids which are in vertical double row systems, with the cloacal canals opening around the upper margin of the head.

INTERNAL STRUCTURE: Zooids are of the usual form, about 2mm long with 12 to 14 stigmata per row. The stomach is slightly obliquely oriented, wide anteriorly and gradually decreasing in diameter toward the pyloric end where it is continuous with the intestine. There is no gastric reservoir in any of the examined material. The gut loop is vertical. The body wall has no papilla over the pyloric end of the stomach. No gonads occur in the newly recorded material. Male gonads were in the specimen from Bass Strait (Herdman 1886). They consist of ovate male follicles (Herdman 1886). In an oblique, almost longitudinal section 5 follicles are seen (Herdman 1886, pl. 17, fig. 10). Specimens from the NSW coast (Kott 1957a) have mature ovaries, embryos and tailed larvae.

The larva has a relatively short trunk 0.7mm long. The 3 adhesive organs, triradially arranged, are on unusually short, thick stalks. The axial cone of adhesive cells with its epidermal cup is particularly large. The tail is long (more than 2mm) and winds around the trunk nearly one and a half times. There are no rudimentary buds in the larval test and the epicardial tube was not detected.

REMARKS: The unique characters of this species are its relatively firm and pigmented test, short stalk that is much the same consistency as the test of the zooid-bearing head, and the size of

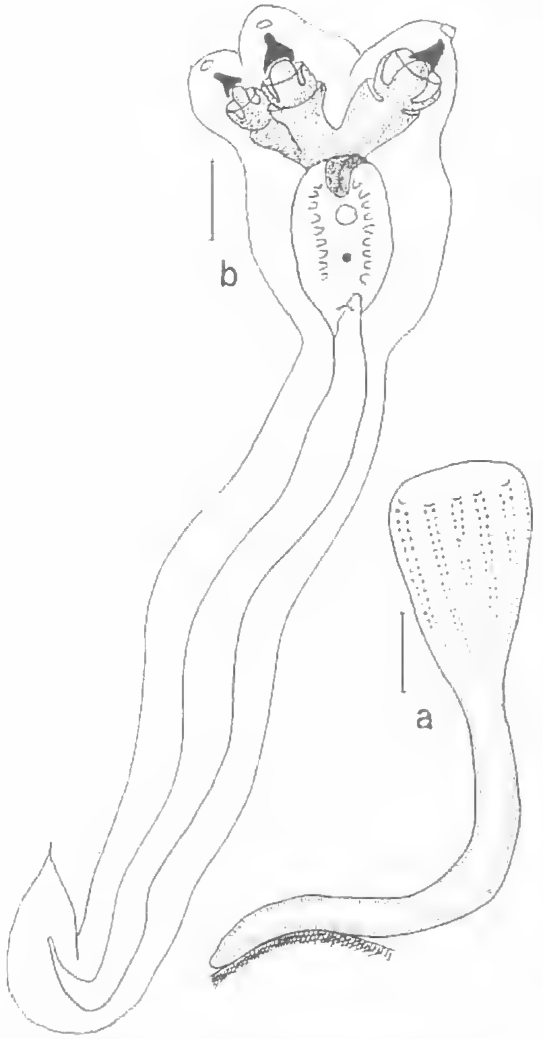


FIG. 54. *Sycozoa murrayi*: a, colony (GH 4155); b larva (AM, off Bermagui). Scales: a, 1cm; b, 0.2mm.

the larva. The large axial cone of cells in the adhesive organs resembles that of *S. cerebriformis*. The head is sometimes flattened as in *S. brevicauda* n. sp., but the stalk is shorter and lacks the terminal hairs of the latter species. *Sycozoa murrayi* is distinguished from *S. pulchra* and *S. pedunculata* by its flattened head with firm test, and its short stalk.

Although the stalk was shorter and thicker than in the newly recorded specimens, Herdman (1886) recorded the characteristically firm pigmented test and flattened colonies in describing this species.

Sycozoa pedunculata (Quoy and Gaimard, 1834)
(Fig. 55, Plate 12b)

Aplidie pedunculatum Quoy and Gaimard, 1834, p. 626.

Not *Aplidium pedunculatum* Cunningham 1871, p. 490 (< *Sycozoa sigillinoides*).

Colella pedunculata: Caullery, 1909, pp. 14, 30 (specimen from King George Sound).

Not *Collela pedunculata* Herdman 1886, p. 74. Pfeffer, 1889, p. 4; 1890, p. 499. Sluiter, 1900, p. 5; 1906, p. 6 (< *Sycozoa sigillinoides*).

Not *Sycozoa pedunculata*: Kott, 1972b, p. 170; 1975, p. 2; 1976, p. 45 (< *Sycozoa pulchra*): Kott, 1972d, p. 243 (< *Sycozoa seiziwadai*).

? *Sycozoa sigillinoides*: Michaelsen, 1924, p. 505 (part, specimens from Tasmania, Bass Strait, Western Port), 1930, p. 505 (part, specimens from Albany).

DISTRIBUTION

NEW RECORDS: Victoria (Portsea, QM G10120; Western Port, AM Y2148; Bass Strait, MV H449, QM G12747) Tasmania (Port Davey, QM GH2022 GH2025; southern Tasmania, TM D708; southeastern Tasmania, TM D2025; Huon Channel, TM D1858; d'Entrecasteaux Channel, TM D276; Derwent Estuary, TM D103, 573 D711 D713 D721-2; northeastern Tasmania, TM D1835).

PREVIOUSLY RECORDED: Western Australia (King George Sound — Quoy and Gaimard 1834, ? Michaelsen 1924, 1930). Victoria (Bass Strait — ? Michaelsen 1924; Western Port — Quoy and Gaimard 1834, ? Michaelsen 1924). Tasmania — ? Michaelsen 1924).

DESCRIPTION

EXTERNAL APPEARANCE. Colonies have an inverted conical zooid-bearing head (up to 2cm long) on a long (up to 9cm), hard stalk. The flat, terminal zooid-free top of the head is from 1 to 1.6cm in diameter, and is the widest part of the head. Basally, the stalk breaks into short branches that attach directly to a hard substrate. Up to 20 zooids in about 20 parallel, vertical double-row systems are evenly spaced around the head. The cloacal canals have wide openings around the outside of the margin of the flat terminal surface of the head. In one colony from Tasmania (TM D708) 5 heads are at the top of the leathery stalk of the colony.

In the specimen from Sandy Bay (TM D711), the central test is withdrawn from the top of the head, leaving zooids embedded in the outer layer of test surrounding a terminal cavity and giving the impression of a terminal common cloaca with a large opening. However, this is an artefact. The cloacal canals open around the outside of head as is characteristic of the present species and not into a terminal cavity as they do in *S. cavernosa* n.sp.

INTERNAL STRUCTURE. Zooids are relatively large for this genus, from 3 to 4mm. The branchial aperture is smooth. The atrial aperture has a wide rounded upper lip. There are 19 or 20 stigmata per row in one specimen (QM G10120), but other

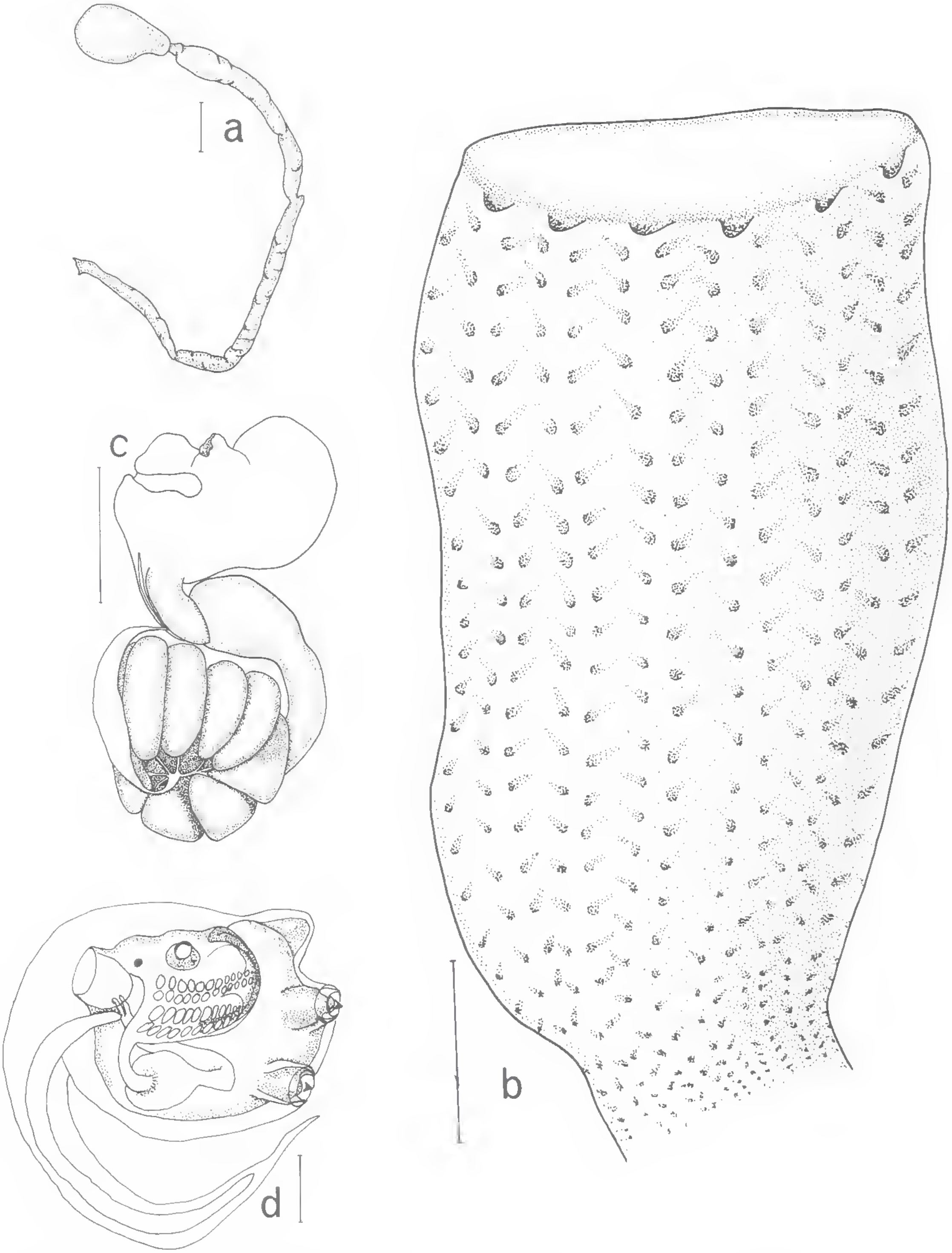


FIG. 55, *Sycozoa pedunculata*: **a**, whole colony (QM GH2022); **b**, head showing arrangement of systems (QM G12747); **c**, male, contracted zooid (TM D708); **d**, larva (TM D711). Scales: **a**, 1cm; **b**, 5mm; **c**, 0.5mm; **d**, 0.2mm.

colonies have only 14 to 16 stigmata per row. The smooth stomach is slightly obliquely oriented. It is wide anteriorly, and posteriorly it tapers to the intestine. Neither a constriction nor a valve is between the intestine and the rectum, that part of the gut distal to the stomach forming an even cylindrical tube. No papilla is present on the body wall over the pyloric end of the stomach. Gonads are enclosed in the gut loop.

The female gonad consists of a large (up to 7-egg) ovary. The mature testis consists of 8 to 10 long follicles arranged in parallel to form a wide, barrel-shaped clump that juts out from the side of the gut loop. The vas deferens makes the usual posterior loop from the distal extremity of the testis before extending anteriorly along the rectum. Mature male gonads are present in colonies collected in September and October from southern Tasmania (TM D708 D2025). In the Bass Strait material one colony (QM G10120) is female with large eggs in the ovary, however embryos are not present. Embryos were in the type specimen (see Caullery 1909, fig. 7, p. 17) and up to 7 embryos are in a brood pouch in the newly recorded material from Sandy Bay (TM D711).

Larvae are relatively small with an almost spherical trunk 0.9mm long. From the newly recorded colony TM D711, larvae from the one brood pouch have tails of variable length. Some, like those of *S. pulchra* reach halfway around the trunk, and others, like those figured by Caullery (1909, fig. 7), reach almost the whole way around the trunk. Neither epicardial tube nor rudimentary buds were detected.

REMARKS: Quoy and Gaimard (1834) described *Aplidle pedunculata* from Western Port (Victoria) and King George Sound (Western Australia). Subsequent authors, including Herdman (1886), recognised it as a species of the genus *Sycozoa* (> *Colella*), but mistook specimens of the Antarctic *S. sigillinoides* Lesson, 1830 for Quoy and Gaimard's species. Accordingly, for many years, *S. pedunculata* was treated as a junior synonym of *S. sigillinoides*. The type material of *S. pedunculata*, from King George Sound was redescribed by Caullery (1909). Although the shape of the colony could cause it to be mistaken for *S. sigillinoides*, larvae of the latter species have a much longer tail.

The short tail (relative to the long one of *S. sigillinoides*) led Kott (1972d) to regard *S. pedunculata* as conspecific with *S. tenuicaulis* (< *S. pulchra*). *Sycozoa pedunculata* is distinguished from *S. pulchra* by its more numerous male follicles, lack of root-like hairs on the base of the stalk and absence of the abdominal papilla. The newly recorded specimens from Bass Strait and Tasmania appear the same species as redescribed by Caullery (1909) from King George Sound, Western Australia.

Sycozoa pulchra (Herdman, 1886)
(Fig. 56, Plate 12c,d)

Colella pulchra Herdman 1886, p. 106; 1891, p. 611; 1898, p. 447.
Sycozoa pulchra: Sluiter, 1909, p. 33. **Not** Van Name 1918, p. 142 (? = *Sycozoa seiziwadae*).
Colella tenuicaulis Herdman 1899, p. 64.
Sycozoa tenuicaulis: Brewin, 1953, p. 57. Kott, 1957a, p. 99; 1972a, p. 8. Millar, 1963a, p. 707.
Sycozoa pedunculata: Kott 1972b, p. 170, 1972c, p. 234, 1976 p. 56, 1975, p. 2.
? *Sycozoa sigillinoides*: Michaelsen, 1930, p. 505 (part, specimens from Fremantle).

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, QM G9476, WAM 1001.83; Cockburn Sound WAM 9577 226.73 102.75 228.82 1002.83, QM G9633; Esperance WAM 68.75), South Australia (Spencer Gulf, SAM E2032 E2034-6 E2046-7; St Vincent Gulf, QM GH216, SAM E2033; Kangaroo I., QM G9999). Victoria (Bass Strait, QM G12745 MV H449; Western Port, MV F53328 F53335). Tasmania (southeastern Tasmania, TM D723 D1172; d'Entrecasteaux Channel, TM D251 D1803 D1858; Roches Beach, TM D1020; Okehampton Bay, TM D1815). Queensland (Moreton Bay, QM G4930 G5140 52; Townsville).

In Moreton Bay (7-8m, Rous Channel), feeding trails of *Dugong dugon* cut through crowded populations (about 2,000 heads per m^2) of this species (A. Preen *pers.comm.*).

PREVIOUSLY RECORDED: Western Australia (Millar 1963a; ? Cockburn Sound Michaelsen 1930). South Australia (Spencer Gulf — Kott 1975; St Vincent Gulf Kott 1972a; Investigator Strait Kott 1972b). Victoria (Portland, Port Phillip Bay, Western Port Bay Millar 1963a, Kott 1976). New South Wales (Botany Bay, Broken Bay, Jervis Bay, Port Stephens, Port Jackson, Bermagui Herdman 1899, Brewin 1953, Kott 1957a, Millar 1963a). Queensland (Moreton Bay — QM G4930 1 G6148-9 Kott 1972c). North Australia (Torres Strait — Herdman 1886). Indonesia (Sluiter 1909).

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are in about 8 pairs of double row systems extending parallel to one another down the sides of vertical, oval or inverted cone-shaped heads, with the terminal, free ends either flattened or rounded, but always without zooids. Deep, V-shaped cloacal apertures open around the side of the upper margin of the head. The stalk is narrow and never is less than 4 times the length of the head, often much longer. A small colony from South Australia, with a head about 1.5cm long, has a stalk of 5cm (SAM E2047), while one from Kangaroo I. (QM G9999)

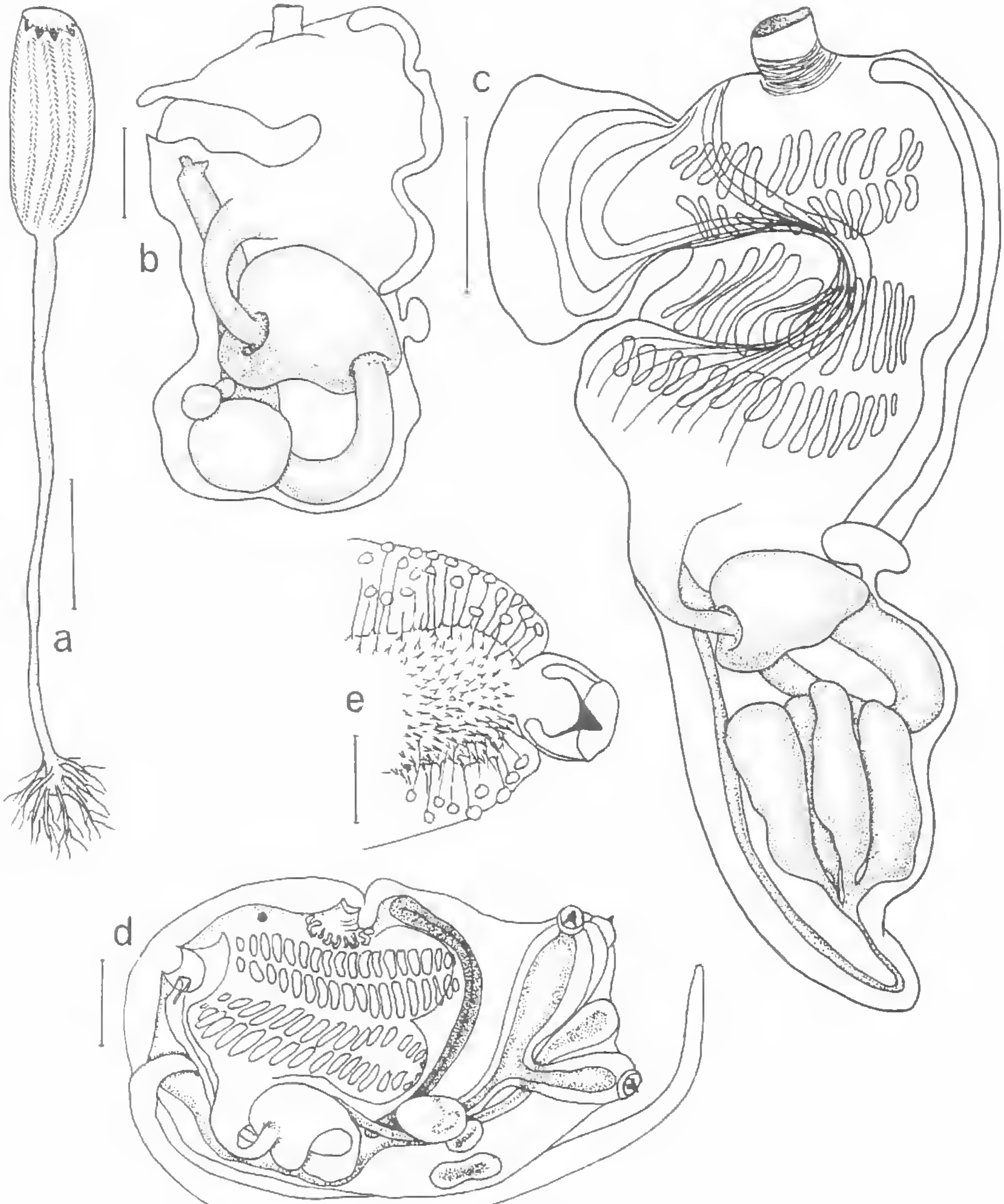


FIG. 56, *Sycozoa pulchra*: **a**, colony (SAM E2047); **b,c**, juvenile and male zooids (SAM E2047); **d**, larva (QM G9261); **e**, detail of larval adhesive organ showing stalked vesicles from epidermis of the adhesive organ stalks (QM G9261). Scales: **a**, 1cm; **b,c**, 0.5mm; **d**, 0.2mm; **e**, 0.05mm.

has a head 5cm long with a stalk of 28cm and is the largest specimen known. A tuft of root-like hairs always is at the base of the stalk, and sometimes tufts of hair occur also at other points along its length. Often several stalked heads arise from a horizontal basal stolon with clumps of hairs scattered along its length. One specimen (WAM 102.75) has a much-branched stalk, each hranch with a small, oval head, and the main stem from which the branches arise has a tuft of roots at its base. The stalk is hard with a hard outer cuticle, but the test of the head is soft. Heads are often found flattened in preservative, but this could be an artefact of preservation resulting from their softness.

Up to 50 functional zooids per row occur in the longer heads, although some of the smaller ones have less than half that number. At the base of the head small replicates, progressively becoming functional, are being added to the systems from the vegetative stolons in the stalk. Headless stalks are often collected (Spencer Gulf SAM E2035–6 collected in November; Moreton Bay QM G5178 collected in October).

Living colonies from Torres Strait were reported as red (Herdman 1886), as are photographed colonies in Cockburn Sound (QM G9633). Specimens from New South Wales were reported as 'yellow, grey, slate, dark purple-brown and dull pale purple' (Brewin 1953, p. 57), however it is not clear that these colours are found in living specimens, although specimens from Moreton Bay are blue. Photographed specimens from South Australia are white to yellow with a red tinge.

INTERNAL STRUCTURE: Zooids without mature gonads are only about 2mm long when the abdomen, which is relatively small, is folded up horizontally behind the thorax as it so often is, even in the small vegetative zooids. The branchial aperture has a smooth margin. The atrial aperture is wide and asymmetrical, with a pronounced upper lip. Muscles are fine, and present only around the apertures. There are 16 stigmata in the anterior pair of rows and 14 in the posterior rows. The most conspicuous feature of all the examined material of this species is the wide knob-like papilla projecting from the body wall, just above the pyloric end of the stomach.

The oesophagus usually makes a right-angled bend before opening into the horizontally oriented stomach, which is wide anteriorly and tapers to its pyloric end before narrowing abruptly to the intestine. The intestine with the rectum forms a continuous cylindrical tube. Gonads are at the side of the gut loop, projecting from it. Thus, when the gut loop is horizontal, the mature gonads project behind it. However, gonads do not project behind the pole of the gut loop. The mature testis contains 4 to 6 long follicles, parallel to one another forming a barrel-shaped clump with its longitudinal axis at right angles to the longitudinal axis of the gut loop. The short vasa efferentia joining the male follicles to the vas deferens are at the distal end of the follicles — the parietal end distant from the gut loop. The vas deferens makes the usual posterior loop before extending anteriorly, down the length of the testis to the rectum. The vas deferens and the rectum extend together to the atrial cavity. Mature ovaries have about 3 eggs.

In upper Spencer Gulf, heads have been observed to detach from the stalks in early summer, another head regenerating the next winter (Shepherd 1983). However, this timetable is not universal, for in other colonies from South Australia gonads are mature in November (SAM E2033) and January (SAM E2034 E2046–7); and embryos occur in the last two specimen lots. In the Tasmanian material embryos occur in July (TM D1815) and December (TM D1172), and maturing ova in October (TM D1803). In the western Australian material mature gonads occur in February (WAM 68.75) and November (WAM 1002.83). In Moreton Bay (Queensland), the gonads are mature in July (QM G5150–2) and September (QM G6148) and embryos occur in April (QM G4930) and July (QM G5151). Thus in South Australia sexual reproduction may occur throughout the summer — from November to February, the heads detaching from early summer to autumn. The existence of sexually mature colonies in April to September in Moreton Bay, suggests a different pattern in the tropics.

From 2 to 8 embryos occur in the brood pouches and half of these are either embryos at an early stage of development or unfertilised eggs.

Larvae are large, the trunk being 1.2mm long. However, the tail is short, wound only a little more than halfway around the trunk. There is an otolith but no ocellus in the cerebral vesicle. The branchial sac is well developed, with 20 stigmata in the anterior rows and 18 in the posterior rows — 4 more in each row than in the adult zooids. The 3 smooth, elliptical stalks of the adhesive organs diverge from one another from the ventral part of the thorax of the oozooid. They contain a conspicuous internal extension of the larval haemocoelic cavity, a layer of ectoderm and a thick layer of test. Cilia-like extensions run through the test from the ectodermal cells. These have small terminal expansions at the outer surface of the test. The axial cone of adhesive cells surrounded by its ectodermal cup and topped with a large hyaline cap is at the end of each stalk. A long extension from the posterior end of the left side of the abdomen — the left epicardial sac — extends forward to lie amongst the stalks of the adhesive organs. It is narrow proximally and expands toward the anterior (distal end). There are 3 rudimentary buds lying in the larval test around the base of this sac, which, presumably, continues its development after the buds separate from it.

Remarks: The range of this species appears continuous from Western Australia across the temperate southern coast to Moreton Bay and Townsville. Consequently there is no geographic reason why *S. tenuicaulis* and *S. pulchra* (from Torres Strait) should be considered distinct. The basal stolon (uniting stalked heads) which Herdman (1899) believed characteristic of *S. tenuicaulis* occurs in temperate as well as tropical populations. Further, the abdominal papilla from the body wall over the pyloric end of the stomach, which Herdman (1886) first reported for *S. pulchra*, is present in all the examined specimens. It appears a reliable taxonomic character supporting the synonymy of *S. pulchra* and *S. tenuicaulis*.

A similar papilla is present in *S. kanzasi* (Oka, 1930) from Sagami Bay. This species, although apparently related, is separated from *S. pulchra* by the presence of a single terminal cloacal aperture (Tokioka 1953). The size differences referred to by Tokioka (1953) and Millar (1975) are not significant, but attributable to zooids and colony of the type specimen of *S. pulchra* coming from the lower end of the range for the species.

Tokioka (1953) believed the papilla in *S. kanzasi* an incipient bud. However there is no indication of budding. In the examined specimens of *S. pulchra* the structure seems a thickening of the ectoderm that is inserted into the test. It may be this device that keeps the gut loop horizontal in this species and in *S. kanzasi*.

Kott (1972c) suggested that *S. sigillinoides*: Michaelsen 1930 from Cockburn Sound is a synonym of *S. pulchra* (> *S. pedunculata*: Kott 1972c). This is probable. *Sycozoa pulchra*, but not *S. pedunculata*, is common in Cockburn Sound (see New Records, above).

The single specimen *Sycozoa pulchra*: Van Name, 1918 from the Philippines has a thicker stalk than is usual for this species, and lacks the papilla on the abdomen. It may not be correctly assigned to *S. pulchra* and probably is a juvenile specimen of *S. seiziwadai*.

The features which together characterise the present species are its knob-like papilla on the abdomen, root-like hairs at the base of the stalk, long, leathery, narrow stalk, small oval to inverted conical head with the cloacal apertures around the outer margin of the top of the head, relatively few male follicles, horizontally oriented abdomen, short-tailed larva, unusual cilia-like extensions from the ectodermal cells of the stalks of the adhesive organs, and long, conspicuous epicardial sac in the larval trunk. Herdman (1899) recorded 8 lobes in the testis of the type material of *S. tenuicaulis*. No more than 6 and often only 4 male follicles have been detected in the course of the present study. Further Herdman reported the position of the gonads as behind the gut loop. This is not absolutely accurate — gonads are always at the side of the gut loop and are posterior to it only when the abdomen is bent at right angles to the thorax, placing the gut loop horizontally.

The closest known relative of the present species is *S. brevicauda* n. sp. which also has root-like hairs at the base of a narrow stalk, a conspicuous epicardial sac in the larva and similar extensions from the ectodermal cells of the stalks of the adhesive organs. However in *S. brevicauda* the head is flattened and fan-shaped, there are more numerous male follicles, no papilla on the abdomen, the larval trunk is half the length of that of *S. pulchra*, and its tail is shorter than that of the present species.

Sycozoa seiziwadai Tokioka, 1952
(Fig. 57a,b)

Sycozoa seiziwadai Tokioka, 1952, p. 99. Millar, 1963a, p. 708; 1975, p. 223.

Sycozoa cerebriformis: Hartmeyer, 1919, f. intermedia p. 121.

Sycozoa pedunculata: Kott, 1972d, p. 243.

? *Sycozoa pulchra*: Van Name, 1918, p. 142.

? *Sycozoa* ? *sigillinoides*: Monniot, 1988, p. 199.

Distribution

New Records: Western Australia (Port Hedland, WAM 189.87; Dampier Archipelago, WAM 1050.83; Cape Preston WAM 802.83). Queensland (Swain Reefs, AM Y2144). Northern Territory (Darwin, QM GH4218, WAM 108.75).

Previously Recorded: Western Australia (Broome, Holothurian Banks, Bassett Smith Reef — Millar 1963a; Cape Jaubert — Hartmeyer 1919). New South Wales (Cronulla — Kott 1972d). Arafura Sea (Tokioka 1952). Philippines (Millar 1975, ? Van Name, 1918).

The record of its occurrence at Cronulla, NSW, is anomalous for this species in view of its otherwise exclusively tropical range. It is recorded subtidally to 40m.

Description

External Appearance: Colonies consist of thick (up to 1cm diameter) branching stalks, the relatively short terminal branches each expanding into a short drum- to fan-shaped zooid-bearing head, circular to oval or elliptical in section, and absolutely flat on the upper surface. The whole colony is firm and gelatinous. The upper surface of the zooid-bearing heads is often indented where the cloacal apertures open around the margin.

Adjacent heads sometimes fuse with one another near the upper surface where they touch.

Zooids are arranged in parallel vertical rows, one each side of a cloacal canal, with from 10 to 15 functional zooids per row and up to 16 double rows per head.

The collector has noted that the newly recorded specimen from Darwin (QM GH4218) was orange with yellow spots and some black in the colony. Faint traces of the yellow spots are present in the surface test of the preserved colony.

INTERNAL STRUCTURE: Zooids are about 3mm long with the thorax and abdomen of about equal length. The branchial aperture has a few, minute, pointed papillae around its border and a thin band of circular muscles. There are also the usual fine muscle bands around the atrial aperture. The large atrial aperture has the usual asymmetry. The branchial sac has 14 stigmata in the anterior pair of rows and 12 in the posterior pair. The stomach, which is slightly smaller than usual in this genus, is more or less vertical, as is the whole gut loop. The stomach is wide at its anterior end and tapers gently toward the pyloric end where it abruptly narrows. The intestine and rectum together form a cylindrical tube of even diameter. The gut loop is relatively long and narrow. A gastric reservoir was not detected.

Gonads are enclosed in the gut loop toward its posterior end where they protrude slightly from the right side. All the mature heads of the available colonies are male. One from Western Australia (WAM 1005.83) was collected in October and one from the Northern Territory (QM GH4218) in August. The testis consists of 6 long follicles forming a barrel-shaped clump, with the short vasa efferentia from each follicle joining the vas deferens at the distal end. The vas deferens makes a posterior loop before extending anteriorly along the rectum to the atrial cavity.

One embryo per brood pouch occurs in specimens from north-western Australia (Millar 1963a). In these larvae the trunk is relatively short (0.6mm) and the tail is wound almost completely around it. Stalks of adhesive organs are wide with a large cone of adhesive cells, which, in its epidermal cup, is depressed into the end of the stalk. Three rudimentary buds are in the larval test.

REMARKS: The colonies of this species have similar fleshy stalks to those of *S. cerebriformis*. However, they are longer than in *S. cerebriformis* and are always branched. The zooid bearing part although often flat is not ribbon-like and pleated as in *S. cerebriformis*, although the tendency for the heads to fuse also occurs in *S. cerebriformis* (see Herdman 1899). Other differences are discussed above (see *S. cerebriformis*). Larvae of the present species are significantly smaller and have a longer tail than those of other temperate or tropical species.

Sycozoa cerebriformis: Hartmeyer, 1919 (f. intermedia) has the characteristically branched stalks of the present species, and the same flattened heads that fuse with one another.

Sycozoa pulchra: Van Name, 1918 from the Philippines has the same shaped head and fleshy stalk of the present species and is very likely a juvenile colony of this species.

Sycozoa? *sigillinoides*: Monniot 1988 from New Caledonia is unlikely to be a specimen of the Antarctic species to which it has been assigned. Since its larva is the same as *S. seiziwadae*, it may be conspecific.

Hartmeyer (1919), Michaelsen (1923) and Millar (1963a) compared characters of *S. cerebriformis* and *S. seiziwadai* with the South African *S. arborescens* Hartmeyer, 1912. The South African species has a terminal cloacal cavity with a central aperture, as in *S. sigillinoides*, thus it must be distinguished from *S. seiziwadai* and *S. cerebriformis*. The branching stalk, each branch with a separate head, occurs in both *S. arborescens* and in the present species.

The present species has a tropical, western Pacific range, not apparently extending into temperate waters — Cronulla, off the New South Wales coast being the most southerly record to date.

Sycozoa sigillinoides Lesson, 1830
(Fig. 57c,d. Plate 12e)

Sycozoa sigillinoides Lesson, 1830, p. 436. Hartmeyer, 1911, p. 534. Michaelsen 1924, p. 288. Salfi, 1925a, p. 2. Van Name, 1945, p. 151. Ärnbäck, 1950, p. 29. Brewin 1952b, p. 190; 1953, p. 56. Kott, 1954, p. 155; 1957a, p. 99; 1969, p. 26; 1971, p. 18. Millar, 1960, p. 71; 1982, p. 12. Not Michaelsen, 1930, p. 505 (? < *Sycozoa pulchra*, *S. pedunculata*).

Colella sigillinoides: Michaelsen, 1907, p. 43.

Sycozoa aff. *sigillinoides*: Hartmeyer, 1911, p. 489.

Sycozoa (*Colella*) *sigillinoides*: Hartmeyer, 1912, p. 313.

Aplidium pedunculatum: Cunningham, 1871, p. 490.

Colella pedunculata: Herdman, 1886, p. 74. Pfeffer, 1889, p. 4(40); 1890, p. 499. Sluiter, 1900, p. 5; 1906, p. 6. Not Caullery, 1909, pp. 30, 39 (< *Sycozoa pedunculata*).

Colella quoyi: Harant and Vernières, 1938, p. 6.

Sycozoa quoyi: Kott 1954, p. 157; 1957c, p. 1.

Colella ramulosa Herdman, 1886, p. 120. Michaelsen, 1907, p. 53.

Colella umbellata Michaelsen, 1898, p. 371; 1907, p. 54 f. typica, p. 59 f. kophameli. Caullery, 1909, p. 53.

Sycozoa (*Colella*) *umbellata*: Sluiter, 1919, p. 12.

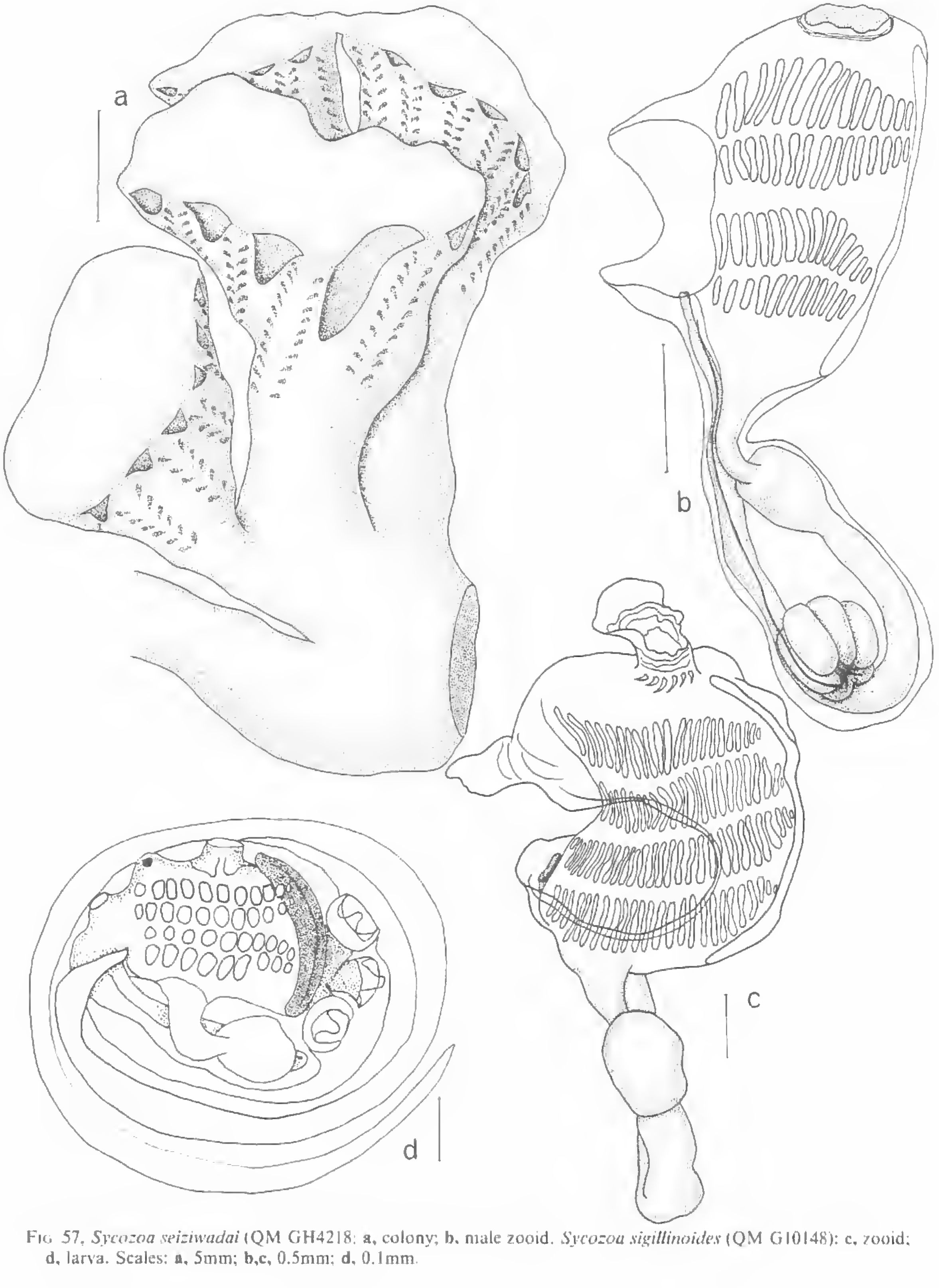


FIG. 57. *Sycozoa seiziwadai* (QM GH4218: **a**, colony; **b**, male zooid. *Sycozoa sigillinoides* (QM G10148): **c**, zooid; **d**, larva. Scales: **a**, 5mm; **b,c**, 0.5mm; **d**, 0.1mm.

Colella perrieri Caullery, 1909, p. 33.
Sycozoa perrieri: Hartmeyer, 1909-11, p. 1439.

DISTRIBUTION

NEW RECORDS: South Australia (southern part of Spencer Gulf, QM GH4171). Tasmania (St. Helens, QM G10148; Montague I., AM G13077).

PREVIOUSLY RECORDED: Antarctic and Sub-antarctic (circumpolar, and north to Magellanic area, Falkland Is. Kerguelen, Heard and Macquarie Is., Chatham I., — see Kott 1969). New Zealand (Michaelsen 1924, Brewin 1952b).

Specimens from Cockburn Sound, Western Australia, assigned to this species by Michaelsen (1930) are probably of *Sycozoa pulchra* as this is the only species now known to occur there. The records from Albany and King George Sound (Western Australia) may be either *S. pulchra* or *S. pedunculata* (type locality).

Records of this species from the tropical Atlantic (Michaelsen 1907) and the tropical Pacific (Michaelsen 1924) Oceans are of isolated heads in the plankton. The tendency for the heads to separate from the stalks and float in the plankton may contribute to the wide geographic range of the species.

The northern limit of the recorded range of this Antarctic species is off South Australia. However, records from Australian waters are rare, and so far the only other Australian localities from which the species has been taken are off Tasmania.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of more or less oval heads (up to 2.5cm long and 1cm in diameter) on long, thin and hard stalks. Stalks taper toward the base where they spread slightly to form leathery holdfasts. Zooids are in parallel double-row systems down the side of the head. The cloacal canals open around the central test core at the top of the head and the outer test is sometimes folded in to cover them, often leaving the central core slightly protruding. In some colonies (QM GH4171), however, the test core at the top of the head is disintegrating, depressed and porous, leaving the zooids embedded in longitudinal ridges of the outer layer of test that project into a central cavity to which the cloacal canals and the atrial apertures of the zooids are exposed (as in *S. cavernosa* n. sp.).

Many of the colonies have branching stalks, with a separate head at the end of each branch. Millar (1960) believed these multiple colonies to have developed following regeneration from persisting stalks.

Living colonies from Tasmania (QM G10148) were orange. In preservative they are cream and one specimen (AM G13077) has orange pigment spots in the surface test.

INTERNAL STRUCTURE: Zooids are relatively large (4 to 5mm long). The branchial aperture has 3 or 4 frills around its ventral side that may appear to be lobes, but actually result from contraction of the branchial sphincter muscle. The whole dorsal border of the aperture is often produced into a large, delicate lobe, into which the muscles of the sphincter spread. The atrial muscles extend out in a similar wide arc in the large, rounded border of the wide atrial aperture. The atrial opening is asymmetrical exposing most of the branchial sac on one side of the body. No muscles are on the thorax except the fine ones around the apertures.

There are from 16 to 26 stigmata per row, the number increasing with the size of the zooids. Small vegetative zooids at the top of the stalk have 16 stigmata in the anterior rows. In one of the newly recorded specimens (QM G10148), which has the maximum number of stigmata, and appears an old colony, the pairing of the rows of stigmata, even in the small vegetative zooids, is not as conspicuous as it usually is, the third and fourth rows being more conspicuously separated ventrally than the second and third rows.

The gut loop is usually vertical: The large brownish stomach is about halfway down the abdomen. It does not reduce in diameter much toward its pyloric end, but it narrows abruptly before opening into the intestine. The intestinal loop is relatively short and the intestine and rectum form a continuous cylindrical tube. Millar (1960) observed a mid-intestinal enlargement but this is not apparent in the present material.

Gonads are at the side of the gut loop, and when mature project from it. Although they are in a sac, it does not have a constriction separating it from the abdomen. Mature gonads are present in both newly recorded specimen lots, collected in April (from South Australia) and October (from Tasmania). Ovaries contain about 10 eggs and 12 to 18 wedge-shaped male-follicles crowd into an almost spherical clump with the vas deferens originating at the outer end of the clump and making the usual posterior loop before extending anteriorly on the rectum. Colonies are dioecious. From 6 to 16 embryos and eggs are in a long brood pouch curved at the end. Embryos are lined up with their longitudinal axis across the brood pouch instead of being end to end with their longitudinal axis parallel to its length.

Larval trunks are from 0.4 to 0.76mm (see Kott 1969) and the tails are wound one and a half times around the trunk. They have large cones of adhesive cells rising from the base of the ectodermal cups in the 3 triradially arranged adhesive organs. These are depressed into the tip of the wide stalks (of the adhesive organs) which form an inflated annular base to each cone of adhesive cells. There is an otolith but no ocellus in the cerebral vesicle.

REMARKS: The characters that separate this species from all others in the genus are its larger zooid with more stigmata, larger gonads with more wedge-shaped male lobes and eggs, and more embryos in the brood pouch. The cloacal opening, which comprises a significant distinction from most other species, is difficult to interpret, especially when the terminal part of the head is disintegrating. However, when this happens, the openings of the cloacal canals appear drawn down inside the head, and the atrial openings are exposed to the inner chamber rather than directly to the exterior as they are in most other species of the genus, except in *S. cavernosa* n. sp. In the latter species the cloacal cavity in the centre of the head indicates a relationship to *S. sigillinoides*.

Sycozoa pulchra and *S. pedunculata* superficially resemble the present species, but are distinguished by their separate cloacal apertures and their short-tailed larvae. The larva of *S. sigillinoides*, like that of *S. murrayi* has relatively large cones of adhesive cells and a long tail.

Family STOMOZOIDAE new family

The family is erected to accommodate a single genus *Stomozoa* Kott, 1957b, formerly regarded as a member of the Clavelinidae. The genus has 6 fringed lobes around each aperture. Pigment spots (possibly ocelli) are present at each side of the base of each of these lobes. A well developed siphonal velum in each siphon projects outwards to form a conical structure with a terminal aperture. There are numerous stigmata and wide transverse vessels, but no internal longitudinal vessels. Long vascular stolons, occasionally branching and terminating blindly in the firm test, lack both a mesodermal septum and terminal ampullae. Longitudinal muscles extend from the apertures and converge into a strong longitudinal band along each side of the ventral mid-line of thorax and abdomen. Relatively small gonads are in the gut loop, the testis with pear- to club-shaped follicles, and the ovary containing only one or at most 2 eggs.

The gonads of this genus often are difficult to see. Those of the 2 new Australian species and the 2 previously described are similar (Millar 1955, Kott 1957b). Millar (1977) reports 'spent gonads' in the Brazilian material of *S. roseola*. However, his figure suggests the small group of male follicles reported may be part of the mass of tangled tubules of the pyloric gland present in the same position in the newly recorded Australian material. The ovary of *S. murrayi*: Monniot, 1988 has more eggs than the one or 2 usually found. Only a single large embryo has ever been found in the atrial cavity of a *Stomozoa* sp. Larvae of Stomozoidae have triradially arranged adhesive organs, 2 dorsal and one ventral, each with a wide and shallow axial cone in an epidermal cup. The test is firm and gelatinous throughout.

Kott (1957b) assigned the genus *Stomozoa* to Clavelinidae, believing the smooth border of the muscular velum homologous with the smooth-rimmed apertures of that family. However, the pigment spots at the base of the lobes around the outside of the apertures suggests these fringed lobes are more likely homologues of the lobed apertures of Diazonidae. Clavelinidae are further distinguished by their soft and flaccid thoracic test, larger ovaries, more numerous embryos incubating in the atrial cavity, and longitudinal thoracic muscles that extend postero-dorsally (rather than postero-ventrally as they do in the present family). Although they lack the clavelinid frontal plate the larvae are generally more like *Clavelina* larvae than those of *Distaplia* (see also Millar 1977).

The present family does not appear closely related to the Holozoidae. The vascular stolon lacks an epicardial septum and any sign of vegetative zooids developing from the narrow vascular stolon as in Holozoidae. Thus it is possible replication could be by transverse division of the zooids as in Diazonidae and Polycitoridae.

Stomozoidae are separated from Diazonidae by the absence of internal longitudinal branchial vessels, large viviparous larvae, and firm test over the upper thoracic part of the colony.

Their closest relatives may be Polycitoridae, as zooids of both have broad ventral muscle bands in the abdomen and a long oesophagus. Stomozoidae are separated from the latter family by the long vascular stolon and larvae with triradially arranged adhesive organs.

Kott (1981) in discussing the relations of *Euherdmania digitata*, and *E. dentatosisphonis*, the latter species with fringed lobes around the apertures similar to those of the present family, thought both may be synonymous with *Stomozoa roseola* (Millar, 1955). However, Millar (1977) had already considered these relationships, and concluded that the presence of gonads in a posterior abdomen and incubating embryos in the abdomen characteristed *Euherdmania* as distinct from *Stomozoa*. Other features distinguish these two genera. In particular, *Euherdmania* has tubular larval adhesive organs, a folded stomach, separate zooids and lacks a vascular stolon. Further, although ocelli are in the centre of the lobes around the apertures of *Euherdmania* they are not at each side as they are in *Stomozoa*. Thus, it appears *Euherdmania* and *Stomozoa* are not closely related and the fringed lobes around the apertures of some *Euherdmania* species may not be homologous with the similar ones in *Stomozoa*.

The small ovary and few large embryos produced in the known species of the present family suggests it has a long evolutionary history as a colonial organism. Available evidence offers no alternative to the hypothesis of early isolation from a diazonid ancestor, possibly in common with Polycitoridae, the latter family diverging from Stomozoidae with loss of the ocelli around the apertures, reduction in size of zooids and larvae, and acquisition of median (rather than triradial) arrangement of larval adhesive organs.

Genus **Stomozoa** Kott, 1957

Type species: *Stomozoa murrayi* Kott, 1957b (< *Clavelina roseola* Millar, 1955).

Since Stomozoidae is monotypic, the generic characters are also those of the family.

There are 3 species. The type species is known from a remarkably wide, albeit tropical, geographic range, *viz.* the Brazilian and Guyana Shelves (< *Diazona gigantea*: Monniot, C., 1970; *S. murrayi*: Millar 1977, 1978), South Africa (*Clavelina roseola* Millar, 1955; *S. murrayi*: Millar 1962), New Caledonia (*S. murrayi*: Monniot, 1988) and the Red Sea (*S. murrayi* Kott, 1957b). No apparent morphological differences in specimens from these locations exist to indicate speciation in either adult colonies or zooids. Larvae are known only from Brazilian populations. Only a single larva is produced at a time by each zooid. Accordingly, the strategies for gene flow are not apparent. Both Australian species described below appear indigenous, one a temperate species recorded on a number of occasions from the Great Australian Bight, the other (from the tropics) recorded once from Heron I. and 4 times from the north-western coast. Both species have fewer stigmata in the adult zooid than *S. roseola*, but otherwise are similar to it. Larvae, known from both, are only half the size of the larvae of *S. roseola*.

Stomozoa australiensis n.sp.

(Fig. 58, Plate 12f)

Distribution

Type Locality: South Australia (Topgallant I. Great Australian Bight, 5m, coll. S.Shepherd 29.3.82, holotype QM GH974; Ward I., Great Australian Bight, cliffs and caves, 6m, coll. S.Shepherd, 12.4.83, paratypes, QM GH946 GH2392).

Further Records. South Australia (Great Australian Bight, QM GH1300).

Description

External Appearance: Colonies are up to 3cm high, and consist of numerous translucent, almost spherical heads up to 1.5cm in diameter, with slightly narrower, opaque stalks joined to one another basally. The internal test is firm and translucent throughout. Some patches of orange pigment cells are around the zooids, and minute (0.02mm) morula bodies are evenly scattered through the test about 0.05mm apart. These are not calcareous. In expanded colonies the large, fringed lobes around the apertures of the zooids protrude from the upper surface, and sometimes the whole anterior portion of each zooid projects. When zooids are withdrawn the upper surface of the colonies is flat. Living colonies are described as bright pink, although photographs do not confirm that description, some variation is likely. Colonies are white in preservative. Epibionts grow amongst the stalks — in one colony a botryllid adheres closely to the test of the stalk.

Internal Structure: Zooids, tightly enclosed in the firm test, are difficult to remove. When contracted they are about 1cm long. The 6 characteristic lobes around each aperture are subdivided into 5 or 6, each subdivision with a terminal narrow point. Orange ocelli are at each side of the base of each of the lobes. The fringed lobes fit into corresponding lobes of the test. The median dorsal lobe of the branchial aperture and the ventral lobe of the atrial aperture are larger than the others. On the thorax about 4 longitudinal muscle bands from the branchial aperture and about 8 altogether from the intersiphonal space and atrial aperture extend toward the ventral border of the zooid where they join into the 2 characteristic wide ventral bands extending the full length of the zooids — one on each side of the ventral midline. The ventral bands extend almost to the posterior end of the abdomen where they terminate abruptly around the posterior vascular stolon where it emerges from the ventral side of the abdomen. In most specimens the strong contraction of the ventral muscle bands has drawn the proximal end of the vascular stolon away from the tip of the abdomen to just opposite the stomach. Anteriorly, the muscles extend into the muscular velum around each aperture. The fringed lobes themselves do not contain conspicuous muscles. About 40 fine branchial tentacles are behind the base of the branchial velum. Thoraces of these specimens are so contracted that it was

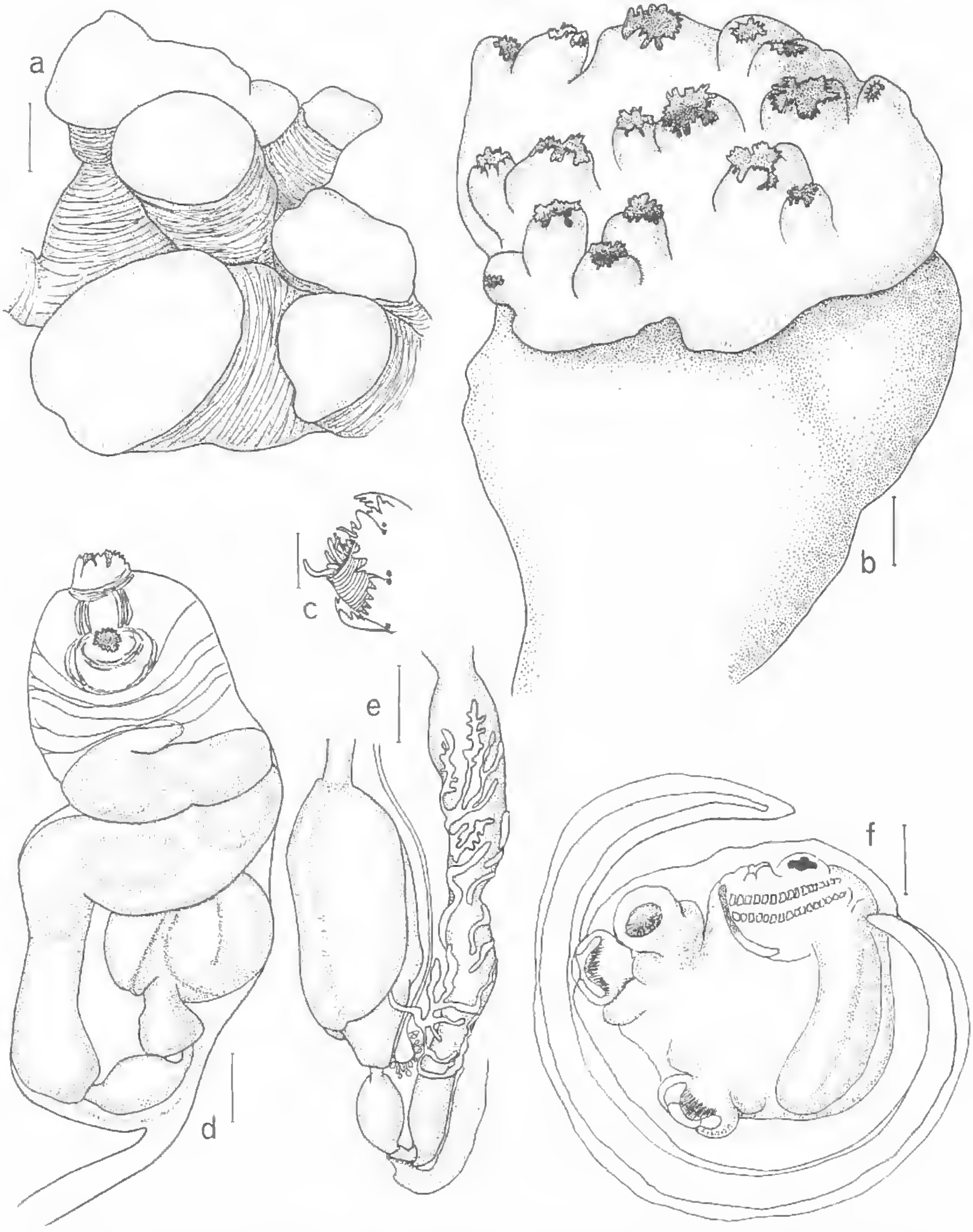


FIG. 58, *Stomozoa australiensis* n.sp.: **a**, general shape of colony (paratype QM GH946); **b**, single lobe of a colony with zooid openings distended (holotype QM GH974); **c**, branchial lobes surrounding muscular aperture through which the tentacles are protruding (holotype QM GH974); **d**, zooid from dorsal surface (paratype QM GH2392); **e**, abdomen showing branches of pyloric gland, ovary surrounded by minute male follicles, and the heart (paratype QM GH946); **f**, larva (paratype QM GH946). Scales: **a,b**, 2mm; **c,f**, 0.2mm; **d,e**, 0.5mm.

not possible to determine whether the tentacles were in one or more than one circle. The opening of the neural gland is circular.

Twelve to 14 rows of long, narrow stigmata, with about 30 per row, are separated from one another by wide transverse membranes. Dorsal languets are wide and dorso-ventrally flattened where the transverse vessels cross the dorsal sinus.

The oesophagus is long, but often is wrinkled owing to contraction of the body muscles. The stomach, in the posterior end of the abdomen, has 6 fine ridges interrupting the glandular lining. An oval posterior stomach is in the descending limb of the gut loop, separated from the stomach by a narrow mid-intestine, usually also obscured by contraction. The anus opens at the base of the atrial cavity. The pyloric gland from the distal end of the stomach divides into numerous branched tubules that encircle the ascending limb of the gut from opposite the stomach to about halfway up the abdomen. A one-egg ovary with apparently a large polar body is on the right side of the gut loop. The testis, beneath the ovary, consists of pear- to club-shaped follicles. Fine-branching vasa efferentia converge to the base of the vas deferens. There is often a mass of minute cells and granular material (that may be associated with the vegetative process) in the loop of the gut and around the outside of the posterior end of the intestine. This material obscures the gonads and the pyloric gland.

In one specimen lot (QM GH946) a single large embryo is in the atrial cavity. The larval trunk is almost spherical, 1mm in diameter. Three rounded ampullae project between the triradially arranged adhesive organs. Each adhesive organ has a wide axial protrusion in an epidermal cup. The tail is wound slightly more than halfway around the trunk. The larval test like that of the adult colony is tough, white and almost opaque.

REMARKS: The species is distinguished from *Stomozoa roseola* (Millar, 1955) by its small number of rows of stigmata, *S. roseola* from the Brazilian Shelf having 26 to 32 rows with up to 60 in a row (Kott 1957b, Millar 1977), and specimens from the Guyana Shelf having 19 or 20 rows (Millar 1978); and by the size of the larvae, that of *S. roseola* (2mm trunk diameter) being about twice the size of the present species. The adhesive organs of the present species are the same as those of *S. roseola*. The rounded swelling Millar (1977) observed on the top of the central knob of cells in the adhesive organs may be a hyaline cap as in *Distaplia* larvae (see Cloney 1977). It is not present in the larvae of *S. australiensis* from South Australia. Otherwise the species are remarkably similar — the colonies, muscle bands, gut and lobes of the apertures all being identical. Spicules in both Red Sea and Brazilian specimens of *S. roseola* are not present in *S. australiensis*. Differences between the 2 Australian species are discussed below.

Stomozoa bellissima n.sp.

(Fig. 59. Plate 12g)

? *Polycitor aurantiacus*: Hartmeyer 1919, p. 108.
Not *Atopogaster aurantiaca* Herdman, 1886.

DISTRIBUTION

TYPE LOCALITY: Western Australia (Bundegi Reef, Exmouth, coll. N. Coleman 14.8.72, AMPI 74, holotype QM G9267). Queensland (Heron I., NE Point 3m, coll. D. Parry 1.11.85, paratype QM GH4918).

FURTHER RECORDS: ? Western Australia (Cape Jaubert — Hartmeyer 1919).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype has a dome shaped head of about 3cm diameter set on a thick stalk of only slightly less diameter. The stalk separates into 4 branches, 2 of which fuse with one another basally to form a thick loop. The head and stalk each occupy about half of the total height (4cm) of the colony. The test is firm but gelatinous throughout, that on the head being translucent, while the outer surface of the stalk is opaque and brownish. The paratype colony is smaller (containing only 8 zooids) with test projecting from the upper surface over the anterior ends of the zooids. As in the holotype, the test becomes firmer toward the base where the diameter of the colony is reduced to form a relatively narrow stalk. Zooids are rather sparsely distributed. They open all around the head and converge in toward the centre and base of the colony. In both specimens they are contracted and withdrawn from the surface. The internal test is firm and contains the long vascular appendages of the zooids irregularly criss-crossing one another.

The test around the apertures is produced into hollow, fringed lobes, which accommodate the lobes of the body wall around the apertures of the zooids. The living specimens have a clear test with poppy red zooids (QM GH4918) or the colony is a pink colour throughout (QM G9267).

INTERNAL STRUCTURE: The contracted zooids are robust and about 1cm long, although in their extended condition they may be up to twice this. The body wall is muscular and siphons and thoraces are contracted in both newly recorded specimens. The branchial aperture is terminal, and the atrial aperture is up to two-thirds of the body length distant from it. The branchial apertures

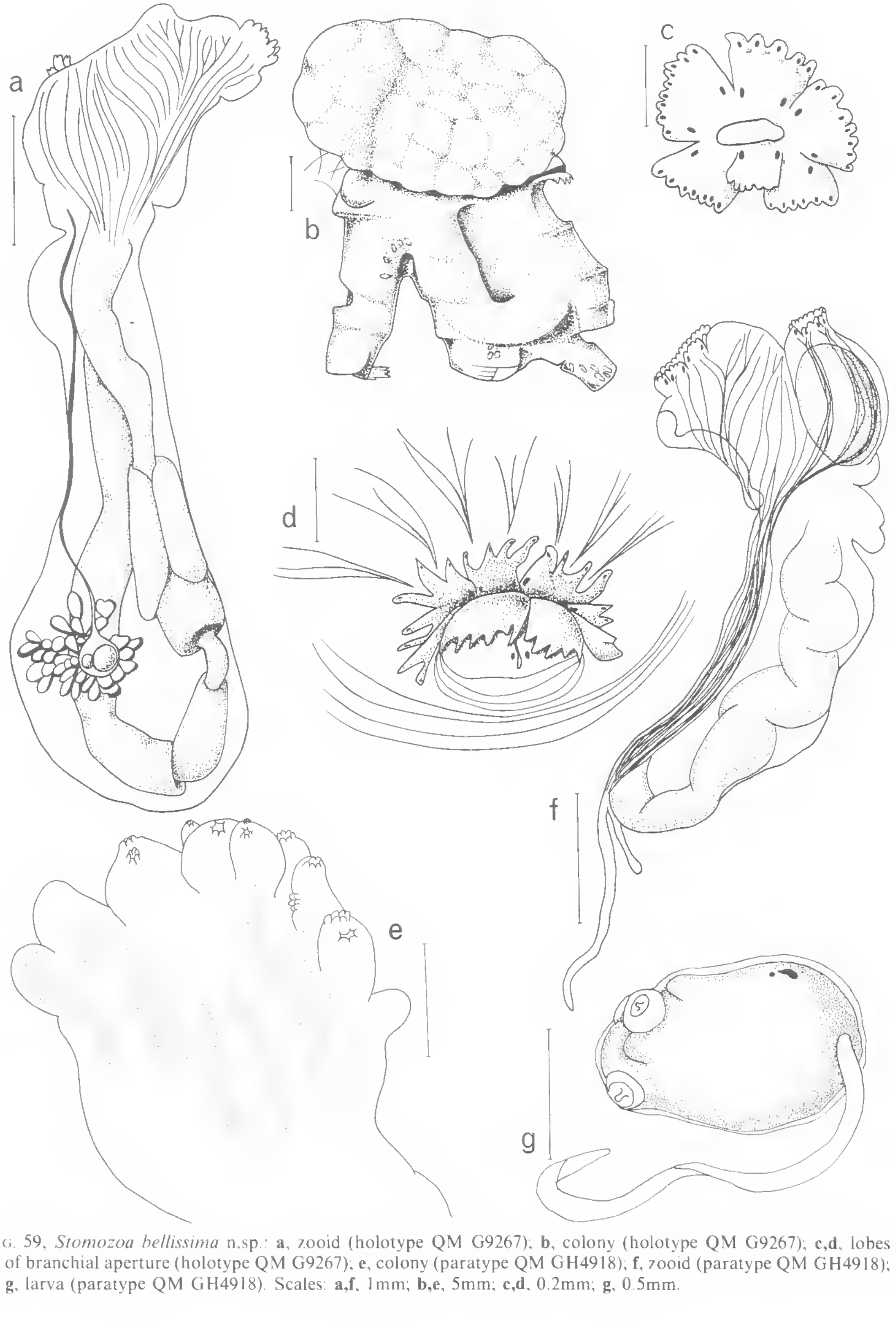


FIG. 59, *Stomozoa bellissima* n.sp.: **a**, zooid (holotype QM G9267); **b**, colony (holotype QM G9267); **c,d**, lobes of branchial aperture (holotype QM G9267); **e**, colony (paratype QM GH4918); **f**, zooid (paratype QM GH4918); **g**, larva (paratype QM GH4918). Scales: **a,f**, 1mm; **b,e**, 5mm; **c,d**, 0.2mm; **g**, 0.5mm.

open below the atrial apertures on the surface of the colony, and the dorsal surface of each zooid is just beneath the surface test.

The border of each aperture is deeply divided into 6 flaps or lobes, each subdivided along its straight or rounded outer edge into a fringe of a variable number of rounded or pointed projections — about 4 on the atrial lobes and up to 8 on the branchial lobes.

Both apertures of the zooids in the holotype colony are transverse. The branchial opening has its 3 largest lobes on the dorsal rim, and in living specimens these probably direct the opening downwards toward the substrate. Four larger lobes are on the posterior rim of the atrial siphon which in some of these contracted zooids folds up anteriorly against the zooid, covering the 2 lobes on the anterior rim. Each of the projections on the outer fringe of each lobe has a small orange pigment spot in the centre. Also a conspicious spherical patch of pigment (possibly an ocellus), yellow in preserved specimens, is on each side of the base of the primary lobes. The latter pigment spots occur in pairs, each located close to its partner on the adjacent lobe. Those on the 3 large dorsal lobes of the branchial aperture and 4 posterior lobes of the atrial aperture are larger than the others. The muscular velum characteristic of this genus is inside each aperture.

A strong band of circular muscles surrounds each aperture. Longitudinal muscle bands radiate from each siphon, but the most numerous muscle bands (at least 15) are those that extend across the dorsal surface between siphons. All longitudinal muscles converge toward the ventral surface to form 2 wide bands extending the whole length of the body, one on each side of the mid-ventral line. Some intersiphonal muscles extend across the dorsal surface just behind the branchial siphon and in front of the atrial siphon. On the ventral side of the branchial siphon, longitudinal bands can be seen radiating away from its base

About 40 crowded branchial tentacles are of various sizes, but all relatively long and slender. The triangular dorsal languets on the dorsal sinus have long points. The thorax is wide, with 14 or 15 rows of about 40 stigmata and wide transverse vessels between the rows.

The oesophagus is long, opening into the rather narrow stomach about two thirds of the distance down the abdomen. The stomach has a suture-line, but although it may be collapsed and appear folded there are no structural grooves or folds in its wall. A wide duodenal area, a narrow, curved mid-intestine and a longish oval posterior stomach are also in the descending limb of the gut loop, and the rectum occupies the whole of the ascending limb. A circular mass of long, almost club-shaped male follicles converge into the centre to join the vas deferens on the right side of the gut loop. A small sac-like ovary with one or 2 ova is outside the male follicles.

A long, fine, vascular appendage, with a few muscle fibres extending along it, projects from the left side of the pole of the gut loop. These vessels have 2 channels, but no mesodermal septum. They resemble the test vessels of Phlebobranchia. They do not run parallel to one another, but criss-cross in the internal test of the colony.

The specimen from Heron I. collected in November has a single larva in the atrial cavity. Its trunk is oval, 1mm long, and the tail is wound about halfway around the trunk. The triradially arranged adhesive organs are the usual sessile shallow depressions with an axial cone. Short ectodermal ampullae alternate with the adhesive organs.

REMARKS. The species differs from the other Australian species of this genus (*S. australiensis* n.sp.) in its posteriorly positioned atrial aperture the more numerous muscles between the siphons, the smooth rather than ridged internal lining of the stomach and oval rather than spherical larval trunk.

The colony of the present species is not broken up into separate lobes as that of *S. australiensis*, although this could be a variable character. The species do have about the same number of long, fine branchial tentacles and rows of stigmata and both have long testis follicles, the same arrangement of their muscles, and the same small, sac-like ovary.

Hartmeyer's specimens from north-western Australia are wrongly assigned to *Polycitor aurantiacus* (Herdman, 1882) from Bass Strait The Bass Strait species has a short oesophagus and a posterior abdomen, and belongs to Polyclinidae. Hartmeyer's specimens had numerous long, fine branchial tentacles, long zooids of about 1.4cm, 15 rows of stigmata and reddish-violet coloured cushion to stalked colony, about 5cm in maximum dimension with the stalk divided basally as in the present colony. Although Hartmeyer records the siphonal lobes deeply separated from one another, he does not describe either a fringe on their outer border, or ocelli at their base Nevertheless, his specimens were contracted, the apertures probably were obscured and it is not impossible that the specimens are of the present species.

Family POLYCITORIDAE Michaelsen, 1904

Colonial, with zooids usually entirely embedded in common test. Zooids are divided into thorax and a long abdomen (containing gut and gonads), and reach almost to the base of the colony. Usually only a short, often branched, vascular appendage is at the posterior end of the abdomen. Both branchial and atrial apertures are 6-lobed, on conspicuous siphons and open separately to the exterior.

Thoracic musculature usually consists of strong external longitudinal bands and an inner layer of transverse muscles. The former continue in two strong bands along the abdomen, one each side of the ventral mid-line. These do not extend on to the posterior abdominal vascular appendix. The usual circular muscles surround each siphon and sometimes (in *Eudistoma*) these form strong conspicuous sphincters. Zooids are particularly contractile. They are often (but not always) arranged in circular systems with the atrial openings in a tight group in the centre of the circle, sometimes in a depression homologous with a rudimentary cloacal cavity. When contracted, zooids appear to detach from the surface test and are withdrawn toward the base of the colony.

Replication is by horizontal strobilation of the abdomen, as in the Diazonidae. Fertilisation apparently is usually in the atrial cavity, and eggs and embryos at different stages of development can be found there. However, in *Cystodytes* and *Polycitorella* and occasionally in *Polycitor* and *Eudistoma* (*Polycitor circes*, *P. annulus* n.sp., *Eudistoma incubitum* n.sp.) fertilisation is at the base of the oviduct, development proceeds as embryos move up the oviduct, and is completed in the atrial cavity or, in some cases, in a brood pouch at the top of the oesophageal neck (see also the Arctic *Polycitor vitreus*: Berrill, 1948a, *Eudistoma clarum*: Van Name, 1945 and *E. olivaceum*: Berrill, 1947b). The 3 larval adhesive organs are in a median vertical line at the anterior end of the larval trunk, except in *Polycitor circes* and *P. annulus* n.sp. (which have them triradially arranged). The adhesive organs are stalked, with a flat-topped cylindrical protrusion of columnar cells in the centre of a cup of specialised epidermal cells, except in *Cystodytes* (in which the protrusion is conical) and in *Brevicollus* n.gen. (which has no axial protrusion). The larval ectoderm is also produced into undivided or bilobed, conical, flattened or cylindrical ampullae in the mid-line (alternating with the adhesive organs), and/or in one to 3 lateral rows along each side of the adhesive organs. Fine extensions from ectodermal cells expand into terminal vesicles in the larval test in some species (see Annotated Glossary: **larvae**). In larvae of this family there are usually 2 rows of stigmata but occasionally 3 (see *E. maculosum* n.sp., *E. muscosum* n.sp., *E. purpureum* n.sp.). The larval tail is especially wide and flat, the trunk contains a large yolk mass, and the larvae give the appearance of being long-lived and strongly swimming.

Polycitorid and holozoid genera were formerly included with clavelinid genera in the Distomidae Giard, 1872 which became a junior synonym of the Polycitoridae Michaelsen, 1904 (after the type genus — *Polycitor* Renier, 1804). Subsequently polycitorid and holozoinid genera were contained in the Polycitorinae of the Clavelinidae (Michaelsen 1930, Huus 1937) until Berrill (1950) separated the holozoids as Holozoinae. In addition to *Distaplia* and *Sycozoa*, Michaelsen (1930) believed the Polycitorinae included *Sigillina* (with subgenera *Archidistoma* Garstang, 1891; *Eudistoma* Caullery, 1909; *Paessleria* Michaelsen, 1907; *Hyperiodistoma* Michaelsen, 1930; *Sigillina*, Savigny, 1816), *Polycitor* Renier, 1804, *Cystodytes* Drasche, 1883 and *Tetrazona* Michaelsen, 1930. Of the subgenera of *Sigillina* (which Michaelsen characterised by the presence of 3 rows of stigmata, and the absence of cloacal systems), *Hyperiodistoma* and *Sigillina*, both with a posterior abdominal vascular appendage containing an extension of the epicardium and with the longitudinal body muscles extending along it, are here considered members of the Holozoidae (see above).

Polycitoridae as defined here contains six genera — *Archidistoma*, *Eudistoma* (including *Paessleria*), *Polycitor* (including *Tetrazona*), *Polycitorella*, *Cystodytes* and 2 new monotypic genera *Brevicollus* n.gen. and *Exostoma* n.gen. Based primarily on replication, phylogenetic affinities of Polycitoridae appear with the Diazonidae, from which it is separated by its smaller embedded zooids without internal longitudinal branchial vessels, smaller gonads, viviparous larvae, and more prolific replication. It also appears related to the Stomozoidae having similar longitudinal muscles forming a pair of ventral bands on the abdomen, and a long oesophagus.

The zooids of *Sigillina*, especially those species lacking muscles on the posterior abdominal vascular appendage (*S. fantasiana*, *S. nigra*), resemble those of *Eudistoma* and *Polycitor* in several ways. This resemblance is enhanced where polycitorid species have a larger than usual vascular stolon (*Eudistoma glaucum*, *E. superlatum* n.sp.). However, the relationships of *Sigillina* spp. to the Polycitoridae do not appear to be close. Polycitoridae are distinguished not only by their method of replication but also by their much smaller zooids, a continuous coat of transverse thoracic muscles, absence of an extensive area of unperforated pharyngeal wall anterior and posterior to the stigmata, and (in all except *Brevicollus* n.gen., *Cystodytes* and *Polycitorella*) a long oesophagus with the stomach at the posterior end of a long abdomen, absence of a stalked brood pouch, and relatively small larvae with small adhesive organs with small circular axial cones rather than the long ridges and platforms found in *Sigillina*.

The two largest genera (*Eudistoma* and *Polycitor*) of the Polycitoridae are similar. *Eudistoma* is distinguished from *Polycitor* by its smaller zooids with short thorax, only 3 rows of stigmata, smaller gonads, and smaller larvae. *Eudistoma* has a characteristic long duodenal region, and small, almost spherical, and always smooth stomach, while *Polycitor* has a short duodenum, and a large and sometimes folded stomach. In *Eudistoma* the anterior row of stigmata is deflected dorsally along each side of the mid-dorsal line — a phenomenon possibly associated with size reduction known in *Pycnoclavella* and *Cystodytes* but not in *Polycitor*. Further, the test of *Polycitor* usually is transparent or translucent while in *Eudistoma* it often is opaque, and with few exceptions, is more brightly coloured than the test of most *Polycitor* spp. *Eudistoma* larval adhesive organs have a thicker axial protrusion than those of *Polycitor*, and more ectodermal ampullae. Zooids are arranged in rudimentary circular systems in *Eudistoma*, *Polycitorella* and *Cystodytes* but only rarely in *Polycitor*. *Polycitorella* and *Cystodytes* also have zooids that resemble one another in having particularly strong muscles. They are distinguished primarily by the form and distribution of calcareous spicules in the test. *Exostoma* n.gen. is unusual in the development of a cloacal system and its zooids are adapted to accommodate that habit. *Brevicollus* n.gen. has many characters that indicate a divergence from the Polycitoridae, and therefore its phylogeny is problematical, and its inclusion in this family is provisional.

Archidistoma is known principally from its type species *A. aggregatum* Garstang, 1891 from the English Channel. Both its zooids and larvae closely resemble those of *Eudistoma*, and Hartmeyer (1924), Van Name (1945) and Berrill (1950) suggested that separate generic status for *Eudistoma* and *Archidistoma* may be unjustified since the only difference between them is the form of the colony — the former species has embedded zooids while those of *Archidistoma* from the type location have zooids almost entirely separate, the basal part of the zooid only being embedded in common basal test. *Eudistoma discederatum* Kott, 1981 from Fiji with zooids separate for at least half of their length resembles colonies assigned to *Archidistoma aggregatum* from the Atlantic coast of North America (Van Name 1945, *fide* Berrill 1950), and Madagascar (Vasseur 1969). In view of the wide geographic range represented by these records, it seems probable similarities in these small colonies are due to convergence, and separate species may be involved. However, at this stage there is no clarification of their generic status. Species such as *E. laysani*, *E. bulbatum* n.sp., and *E. murrayi* Kott, 1957a with the anterior ends of the zooids protruding from the colony represent an intermediate condition which tends to support the view that the genera are synonymous. *Archidistoma* has priority over *Eudistoma*, in the event that they are synonyms.

The family affinities of Japanese colonies (*Archidistoma aggregatum*: Nakauchi, 1960, 1966) with zooids almost entirely embedded, and prominent posterior abdominal vascular stolons are uncertain. Specimens from New Caledonia assigned to the genus *Archidistoma* by F. Monniot (1988) are species of *Pycnoclavella* (see above).

Eudistoma and *Polycitor* are well represented in Australia with both indigenous and Indo-West Pacific representatives. The cosmopolitan *Cystodytes dellachiajei* also occurs around the Australian continent, and there are 2 indigenous species of *Polycitorella*. The family is not well represented in Antarctic waters, and despite the relatively high numbers of Australian indigenous species in temperate waters it is probable that its origin is in the tropics, where it abounds.

KEY TO THE GENERA OF POLYCITORIDAE
(* not recorded from Australia)

1. Cloacal systems extensive . . . *Exostoma* n.gen.
   Cloacal systems rudimentary or absent 2
2. Stigmata in 3 rows 3
   Stigmata in > 3 rows 4
3. Zooids separate . . . . * *Archidistoma*
   Zooids embedded . . . . *Eudistoma*
4. Calcareous spicules present in the test 5
   Calcareous spicules not present in the test . . 6
5. Stigmata in 4 rows . . . . *Cystodytes*
   Stigmata in > 4 rows . . . . *Polycitorella*
6. Parastigmatic vessels present . . . .
   . . . . *Brevicollus* n.gen.
   Parastigmatic vessels not present . . . *Polycitor*

TABLE 7. Summary of Characters of the Species *Polycitor* Recorded from Australia

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Colour (living)	Stigmata (rows;number row)	Stomach	Larval trunk (length mm)	Incubation (location; no. of embryos)	Other
P. calamus n.sp.	A,te	Spencer Gulf, SA–Botany Bay NSW	long cylindrical stalk, oval head	red head	9–13;35	12 folds	?	?	
P. cerasus n.sp	A,te	South Australia	dome-shaped sessile	red	10;25	8 folds	?	?	
P. nubilus n.sp.	A,tc	South Australia	spherical head on short thick stalk	cream	11;20	15 folds	?	?	
P. annulus n.sp.	A,tr	Capricorn Gp; Swain Reefs	mushroom-like head on short, thick stalk (small)	test transparent black zooids	8–10;20	12–15	0.8	abdomen; 1	triradially arranged adhesive organs
P. circes	WP,tr	Martha Ridgeway Rf–Cockburn Snd	mushroom-like head on short, thick stalk (massive)	"	18 23;50	20–30 folds	2.5	"	triradially arranged adhesive organs branchial sac narrows posteriorly
P. giganteus	A,tr-te	Port Hedland–New South Wales	massive spherical or irregular	test transparent; white-orange zooids	12–16; 30–40	4 folds	1.4	atrial cavity; 12	branchial sac narrows posteriorly
P. translucidus	WP,tr-te	Shark Bay–Heron I.	upright cylindrical-rounded lobes	test transparent; yellow-orange zooids	8–10; 20–30	smooth	0.6–0.8	atrial cavity; 3–4	—
P. emergens n.sp.	A,te	New South Wales	upright cylindrical lobes	?	8;20	"	?	?	sandy test; basal half of lobes divided
P. subarborensis	A,te	New South Wales	dome-shaped	?	8;20	"	?	?	"
P. obeliscus	A,te	South Australia	conical sessile	?	6;12	"	?	?	embedded sand

[1]A, indigenous; WP, western Pacific; IWP, Indo-West Pacific; tr, tropical; te, temperate. [2]Range given anticlockwise around the continent.

Genus **Polycitor** Renier, 1804

Type species: *Polycitor crystallinus* Renier, 1804

Species of this genus have relatively large zooids with a long oesophageal neck more than twice the length of the thorax. The rounded stomach is in the descending limb of the gut at the posterior end of the abdomen. There are from 4 to 20 or more rows of stigmata. Parastigmatic vessels are not present. Zooids are completely embedded in firm test. Colonies are stalked or sessile and cushion-shaped, upright or spherical. They range in size from only 1 or 2cm in diameter to about 15cm. Zooids are invariably relatively long, with a long oesophageal neck. They stretch from the surface of the colony to the base. In sessile, rounded colonies zooids converge to the centre of the base where the colony is fixed to the substrate. In preservative zooids are invariably found contracted and drawn away from the surface. Body musculature consists of longitudinal bands extending from each of the siphons, along the thorax and onto the abdomen forming 2 wide ventral bands. Circular sphincters surround each siphon. An internal layer of circular muscles on the thorax sometimes is inconspicuous. Six to 12 branchial tentacles alternate with a variable number of smaller ones in a circle slightly anterior to the larger ones.

Larvae usually have a trunk of about 1mm, although sometimes (*P. circes*, *P. giganteus*) it is longer. Ectodermal ampullae are median, sometimes bilobed and alternate with adhesive organs. The central protrusion of the adhesive organs is narrow and cylindrical. Adhesive organs sometimes are arranged triradially (*P. annulus* n.sp., *P. circes*).

The genus *Distomus* Savigny, 1816 is a junior synonym of *Polycitor* Renier, 1804. Savigny's name is also preoccupied by *Distomus* Gaertner, 1774, a synonym of *Amphicarpa* (Styelinae) (see Michaelsen 1904).

Polycitor is relatively diverse in temperate Australian waters being represented by 6 indigenous species. Only 3 species, *viz. P. circes*, *P. annulus* n.sp. and *P. translucidus* are known from tropical waters. Only the latter has been recorded from elsewhere in the Pacific. *Polycitor circes* and *P. annulus* are among the few tropical indigenous species known in any family of the Ascidiacea. Nine of the 10 species known from Australia are indigenous.

KEY TO THE SPECIES OF *POLYCITOR* RECORDED FROM AUSTRALIA

1. Stomach with > 4 parallel structural folds . . 2
   Stomach with 4 or no structural folds 6
2. Colony with long cylindrical stalk . . . . *P. calamus* n.sp.
   Colony without long cylindrical stalk 3
3. Stomach with 20 or more stomach folds and more than 15 longitudinal thoracic muscles . . . . *P. circes*
   Stomach with less than 20 stomach folds and less than 15 longitudinal thoracic muscles 4
4. Transverse thoracic muscles conspicuous . . . . *P. cerasus* n.sp.
   Transverse thoracic muscles not conspicuous 5
5. Colony transparent with black zooids . . . . *P. annulus* n.sp.
   Colony opaque with whitish zooids . . . . *P. nubilus* n.sp.
6. Stigmata in 10 or more rows; 4 stomach folds . . . . *P. giganteus*
   Stigmata in < 10 rows; stomach without folds 7
7. Base of colony entire 8
   Base of colony divided 9
8. Stigmata in 6 rows . . . . *P. obeliscus*
   Stigmata in > 6 rows . . . . *P. translucidus*
9. Base of colony divided into regular branches, each branch containing a single zooid . . . . . *P. subarborensis*
   Base of colony divided into irregular branches, each branch containing up to 3 zooids . . . . *P. emergens* n.sp.

The species collected by the Siboga Expedition that Sluiter (1909) described as *Polycitor* have only 3 rows of stigmata. Most are *Eudistoma* spp., and these and others are referred to in the discussion of that genus (see below).

Polycitor annulus n.sp.
(Fig. 60)

? *Polycitor circes*: Millar, 1975, p. 205 (part, specimen from the Philippines ZMC 20.iii.41).

DISTRIBUTION

TYPE LOCALITY Queensland (Capricorn Group, Heron I., under rubble near reef edge, low tide, coll. P. Kott May 1987, holotype QM GH4350; Wistari Reef, September 1984, paratypes QM GH4348; Wistari Reef, November 1986, paratypes QM GH4351; Heron I., May 1987, paratypes QM GH4356).

FURTHER RECORDS: Queensland (Heron I., QM GH4346 7 GH4349 GH4352 GH4354 5 GH4433 GH4472 GH4582; Wistari Reef, QM GH4353 GH4434; Swain Reefs, QM GH4346).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are small, wedge-shaped lobes up to 1cm high. In life the upper surface is convex with zooids projecting

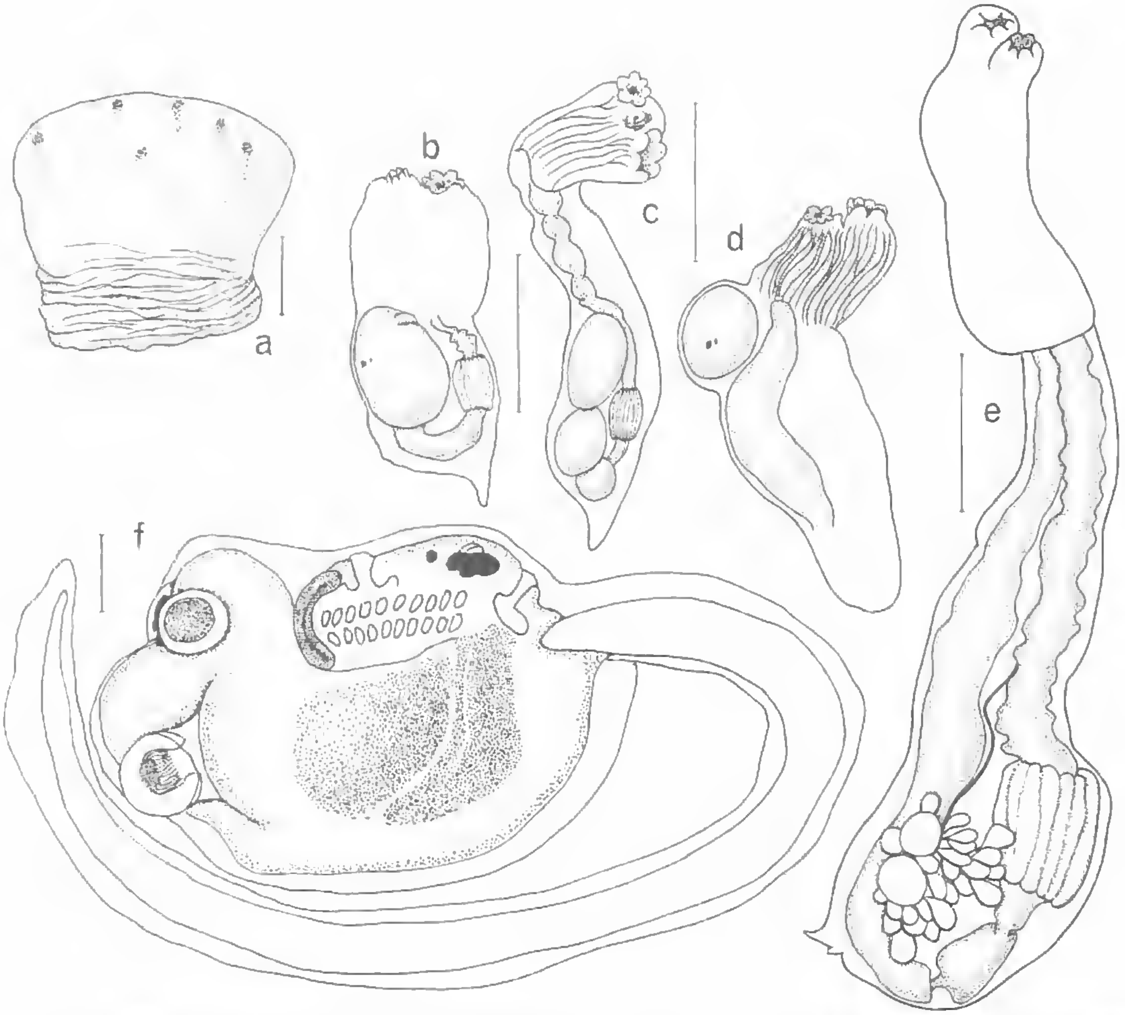


FIG. 60. *Polycitor annulus* n.sp.: a, colony (paratype QM GH4348); b–d, zooids showing incubating embryos (holotype QM GH4350); e, zooid showing gut loop and gonads (paratype QM GH4348); f, larva (QM GH4472). Scales: a, 5mm; b–e, 1mm; f, 0.1mm.

slightly from the surface, their openings showing as black circles in clear, transparent, glassy test. Zooids themselves are black, becoming blackish green in preservative and retaining that colour over a long period in alcohol. The test is soft and may become slightly cloudy in preservative.

INTERNAL STRUCTURE: Small zooids, even when narcotised, contract away from the surface of the colony. Zooids contain dark pigment, concentrated in patches behind the neural complex, around the base of the branchial siphon, over the anterior end of the endostyle, and in longitudinal bands down the length of the thorax. Each aperture has 6 rounded lobes. The thorax is muscular with about 18 parallel longitudinal bands extending onto the abdomen as 2 wide ventral bands. There are 8 to 10 rows of rectangular stigmata with about 20 per row — although, owing to the contraction, these are difficult to count.

The oesophagus is long, but found wrinkled and contracted in all zooids examined; and, also as a result of contraction, the rectum is pleated and folded along its length. The stomach, in the posterior end of the abdomen, is usually obscured by the rectum and by large embryos that start their development at the base of the oviduct. The stomach is short and broad with 12 to 15 shallow, parallel, internal longitudinal ridges. Gonads are present in the gut loop. They consist of a fairly large cluster of relatively large male follicles and a 4- or 5-egg ovary. Although up to 3 embryos can be found moving up the abdomen, only one appears mature at a time and is found just behind the postero-dorsal corner of the thorax, projecting from the top of the oesophageal neck. Neither embryos nor larvae have been found in the thorax. Apparently fertilisation occurs at the base of the oviduct.

In the Capricorn Group mature gonads were observed only in specimens collected in September (QM GH4348). However, developing embryos are present in May (QM GH4350) and March (QM GH4347). Thus, although neither mature gonads nor embryos were seen in specimens collected in October or November, breeding apparently occurs intermittently through the year. Larvae are large in relation to the size of zooids, the trunk being about 0.8mm long. The tail is wound about three-quarters of the way around the trunk. There is an ocellus and otolith. The 3 anterior adhesive organs have relatively short, thick stalks, and a short, relatively thick, flat-topped axial protrusion set in the usual epidermal cup. The adhesive organs are triradially arranged rather than being in the median line. The larval epidermis at the base of their stalks is expanded into rounded swellings.

REMARKS: Superficially this species resembles *Sigillina signifera* in the distribution of pigment in its dark zooids, and transparent test. However, colonies and zooids are both smaller, and zooids lack a posterior abdominal stolon.

This species is characteristically polycitorid in all its characters except for the retention of the large larvae in the abdomen and the triradial arrangement of the adhesive organs — as in *P. circes* (see below). The former possibly is due to the size reduction of zooids without an associated reduction in the size of the larvae. The triradial arrangement of adhesive organs may be a primitive character retained in these species but lost in most species of the Polycitoridae.

Polycitor circes resembles the present species also in the large number of longitudinal thoracic muscles, although it has more stomach folds and about twice the number of rows of stigmata.

One of the specimens from the Philippines (ZMC 20.iii.41) assigned to *P. circes* by Millar (1975) has similar zooids and colony to those of the present species. However, although it broods larvae in the abdomen, and has triradial adhesive organs as in *P. annulus*, the larval trunk is much larger (2.5mm) and despite the small colonies, specimens probably are correctly assigned.

Polycitor calamus n.sp.

(Fig. 61. Plate 13a,b)

DISTRIBUTION

TYPE LOCALITY: South Australia (Archipelago Cove 40m, coll. W. Zeidler 28.1.82, holotype SAM E2058, paratypes SAM E2051; Great Australian Bight, Flinders I. in *Posidonia* 8m, coll. N. Holmes 11.4.83, photo index PE0054 R998, paratype SAM E2057; Great Australian Bight, Avoid Bay 15–20m, coll. N. Holmes and S. Shepherd 9.4.87, paratypes QM GH4187–8 GH4308).

FURTHER RECORDS: South Australia (Spencer Gulf, SAM E2052–6). New South Wales (Kurnell Peninsula, AM Y2197).

The species is common in *Posidonia* beds.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are robust, firm, cylindrical stalks up to 10cm long and 1.5cm diameter with a short spherical to conical head of slightly greater diameter than the stalk. The test of the stalk is transversely wrinkled, almost completely opaque. It narrows slightly toward the base, where its outer surface often becomes quite

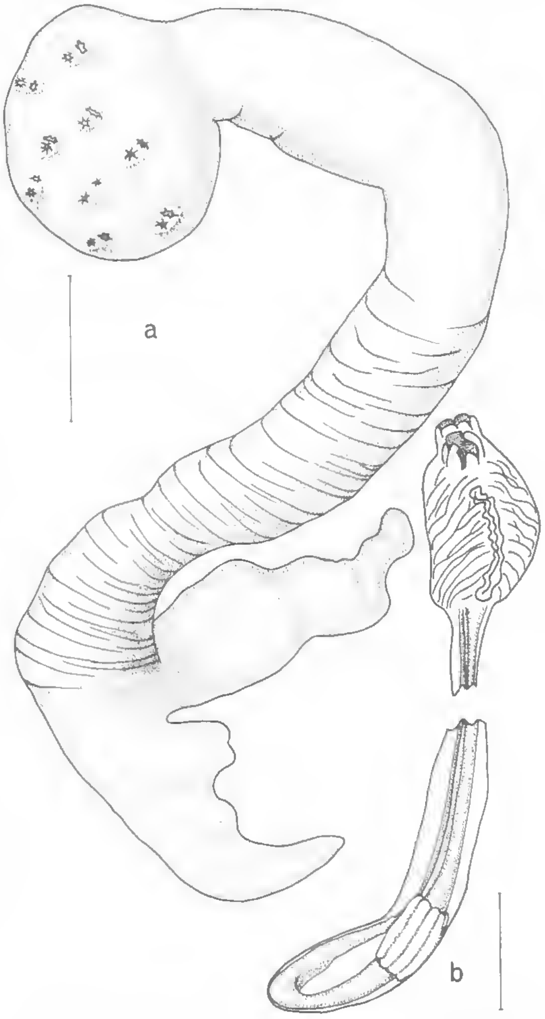


FIG 61, *Polycitor calamus* n.sp. (paratype QM GH4308): **a**, colony; **b**, zooid, part of oesophageal neck excised. Scales: **a**, 5mm; **b**, 2mm.

leathery. Basally the test spreads out into flat holdfasts over the hard substrates, such as scallop shells, to which the colonies are attached. One or more stalks can arise from the basal test, and occasionally a stalk divides into two branches at about one third of its length from the base. The test of the head is gelatinous and translucent in preservative, and in life a bright vermilion. Patches of pigment remain on the surface of preserved specimens. Zooids, only up to 20 per colony, open around the head.

INTERNAL STRUCTURE: Zooids are long, extending from the surface of the head to the base of the stalk. In all preserved colonies the thorax of the contracted zooids is withdrawn from the head down into the stalk. Apertures are close together. Both have 6 well-defined lobes, those on the dorsal rim of the branchial aperture being larger than the ventral ones, suggesting the aperture is directed away from the atrial aperture in life. The body musculature is oblique to longitudinal, resembling clavelinids, with a formula 8E,5B,2A. The muscles run obliquely toward the postero-dorsal corner of the thorax where they extend in two strong bands along each side of the long narrow oesophageal neck that occupies most of the length of the zooid.

In the preserved zooids, 6 large coiled branchial tentacles are behind about 12 shorter, rather stumpy ones. The neural ganglion and gland are both large and oval. The neural duct is short and wide, opening in a simple, circular, anteriorly directed aperture in the prebranchial area. There are 9 to 13 rows of long rectangular stigmata with about 35 in each row. Transverse sinuses between the rows of stigmata extend out into long pointed dorsal languets over the large and conspicuous dorsal sinus that interrupts the rows of stigmata in the mid-dorsal line along the length of the pharynx. Dorsal languets are not flattened, and parastigmatic vessels are absent. A short unperforated area of pharyngeal wall lies anterior to the stigmata.

The relatively small stomach is in the posterior end of the abdomen. It has 12 distinct rounded folds along its length. No subdivisions of the long post-pyloric part of the gut were detected in these specimens, nor were gonads, although vegetative cells were in the abdominal wall suggesting a vegetative phase. Only one colony (SAM E2052) had abdominal strobilae.

A juvenile colony with 4 zooids was taken in January from South Australia. Most other specimens were collected in January, one lot in April (SAM E2057) and the specimen from New South Wales in May. Data suggest a restricted autumn breeding season, and replication from January until the winter months.

REMARKS: The species is distinctive and readily identified by its small, vermilion head, long stalk and particularly long oesophageal neck. All of these characters, together with the absence of circular muscles, readily distinguish it from *Polycitor cerasus* n.sp., which is cherry red in life, and sessile. It differs from most *Polycitor* in having oblique muscles.

Polycitor cerasus n.sp.

(Fig. 62a. Plate 13c)

DISTRIBUTION

TYPE LOCALITY: South Australia (Nuyts Archipelago, Franklin I., loc. c Breaking Reef, 15m amongst algae, coll. N. Holmes 22.2.83, photo index PE044 R811 holotype SAM E2080, paratype QM GH4365).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Only the type material is available. Colonies are sessile and dome-shaped, about 3cm high and 2.5cm diameter. All the test, except the outer 0.5cm thick layer over the upper surface, is crowded with sand particles, making it hard. A little sand is also present in the outer layer of test between the zooids. Zooids converge towards the centre of the colony, from the outer surface. Living colonies are cherry red, although this is lost in preservative.

The lower part of the colony probably is buried in sand, and irregular, sandy extensions from around the periphery of the basal surface probably help to anchor it.

INTERNAL STRUCTURE: Zooids are robust, and, in this type material, about 1cm long contracted. Apertures are both anterior, and open separately to the outer surface of the colony. The rim of each aperture is deeply divided into 6 distinct lobes. The body wall is muscular with an almost continuous but thin outer layer of longitudinal bands, and a conspicuous inner layer of circular fibres. Longitudinal muscles form the usual wide ventral bands of muscle along the abdomen. Triangular dorsal languets are relatively narrow and have a long tapering point. There are 10 rows of about 25 stigmata. The stomach, just over halfway down the abdomen in these contracted specimens, has 8 rather irregular folds in the right (parietal) side. A post-pyloric duodenal area exists, and a short oval posterior stomach is constricted off before the rectum bends around in the pole of the gut loop.

Gonads consist of an extensive, rather diffuse mass of pyriform follicles and a few large eggs on the right side of the gut loop. Male follicles

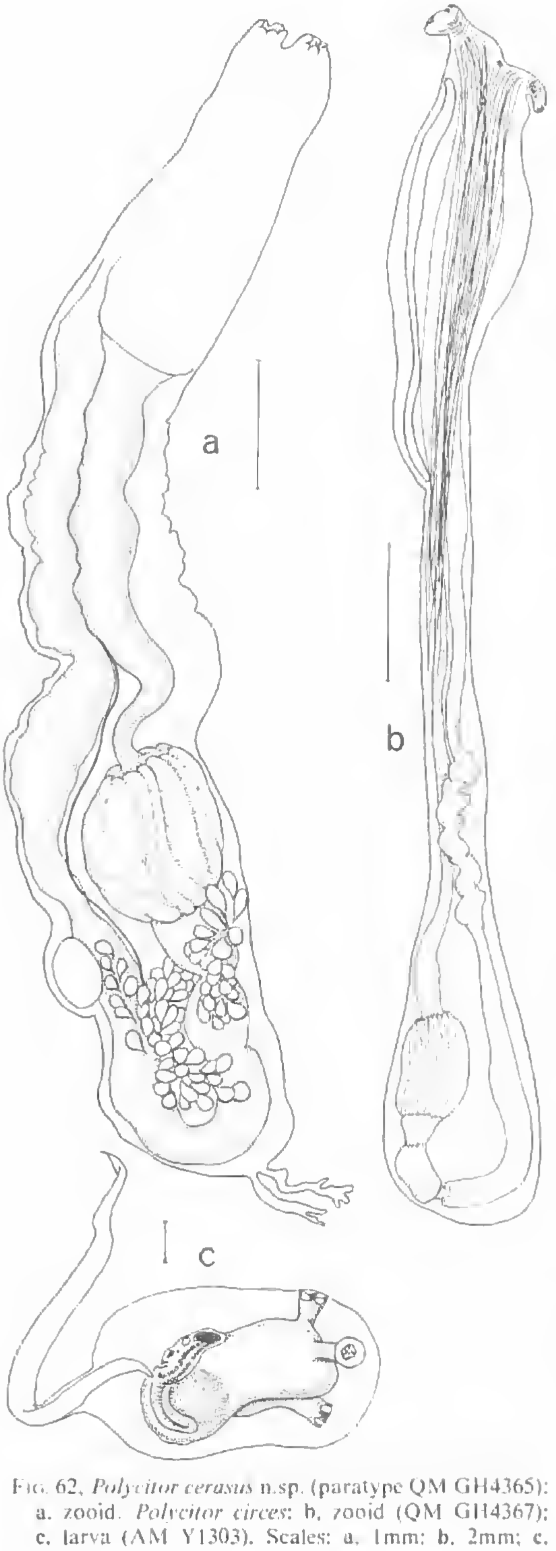


FIG. 62, *Polycitor cerasus* n.sp. (paratype QM GH4365): a. zooid. *Polycitor circes*: b. zooid (QM GH4367); c. larva (AM Y1303). Scales: a. 1mm; b. 2mm; c. 0.3mm.

spread through the loop onto the left side. Two short, branching blood vessels project from the posterior end of the zooid.

REMARKS: The species is unusual in having a mass of sand embedded in the test, making the colony hard to see and obscuring its colour. Similar relatively large zooids converging toward the base of the colony occur in many other species of this genus (e.g. *P. nubilus* n.sp., *P. circes* and *P. annulus* n.sp.). The present species lacks the dark pigment found in the preserved specimens of *P. circes* and *P. annulus*. Colonies resemble those of *P. obeliscus* in their general form, sessile habit, and the distribution of sand within the colony. Zooids of the present species with their folded stomach distinguish it from *P. obeliscus*.

Polycitor circes Michaelsen, 1930
(Fig. 62b,c)

Polycitor circes Michaelsen, 1930, p. 495. Kott 1957a, p. 84; ? 1966, p. 281. Millar 1963a, p. 710; 1975, p. 205 (? part, specimen from Marongas 20.3.1914). Monniot 1988, p. 207.

Polycitor gelatinosa Kott, 1957a, p. 83 (part, not specimens from South Australia).

? *Polycitor renziwadai* Tokioka, 1952, p.96.

DISTRIBUTION

NEW RECORDS: Western Australia (Passage I., WAM 1039.83; Broome, AM Y2192 Y2199; Dampier Archipelago, WAM 1035.83 1042.83; Cervantes Reef, WAM 178.87 180.87; Houtmans Abrolhos, WAM 367.80 *QM GH2110*, WAM 199.88, AM Y2191 Y2195; Cockburn Sound WAM 1036.83). Queensland (Martha Ridgeway Reef, QM GH4367).

PREVIOUSLY RECORDED: Western Australia (Cape Boileau, Broome — Millar 1963a; Cape Inscription — AM Y1292 Kott 1957a; Shark Bay — Michaelsen 1930; Cockburn Sound — Michaelsen 1930; AM Y1302 Y1306 Y1309-10 *P. gelatinosa* Kott, 1957a). New Caledonia (Monniot 1988). Philippines (Millar 1975).

Although there is a preponderance of records from north-western Australia, the newly recorded specimen from Queensland suggests the species will be recorded from other tropical locations in the western Pacific. It is large, conspicuous, and not likely to be overlooked.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are large up to 9cm high and 7cm in diameter, sometimes almost flat-topped but at other times mushroom to club-shaped, narrowing toward the base where there usually is a short, thick stalk, devoid of zooid openings. Otherwise zooids open on the upper surface and sometimes on the sides of the colony and converge toward the top of the stalk. One colony (QM GH4367) is spherical, fixed by a small part of the base, but with zooid openings only on the upper half of the surface. The test is firm, gelatinous and translucent. In preservative zooids are dark blue.

INTERNAL STRUCTURE: Zooids are robust, measuring about 2cm in length even in a contracted state. In preservative zooids have dark pigment, especially in the thoracic body wall and transverse branchial vessels, and forming a conspicuous patch at the anterior end of the endostyle. Branchial and atrial lobes, 6 of each, are rounded. The body musculature is strong, consisting of about 20 longitudinal bands that extend along the abdomen as two wide ventral bands. The usual circular muscles are around each of the siphons, however the inner layer of transverse muscles is inconspicuous. Six large but stumpy branchial tentacles alternate with 3 smaller ones. The neural ganglion is large and spherical. The duct of the neural gland is short and the opening is circular and directed anteriorly. The dorsal languets are long and tapering. In the pharyngeal wall a wide, unperforated area exists anterior to the 18 to 23 rows of stigmata. Up to 50 stigmata in the anterior rows are reduced to about half that number posteriorly.

The oesophagus is long, and invariably is wrinkled in these contracted zooids. It opens into the small, rounded stomach in the posterior end of the abdomen. The stomach wall has 20 to 30 narrow, parallel longitudinal folds. A constriction between an inconspicuous posterior stomach and the rectum is in the pole of the gut loop. The anal border is divided into two large smooth lips. Gonads, a mass of pyriform male follicles with a 3 or 4 egg ovary, are in the gut loop posterior to the stomach.

Ova are fertilised at the base of the oviduct and develop as they move up the abdomen. Their incubation is completed in the top of the abdomen just posterior to the atrial cavity rather than in the atrial cavity as in most other species of the genus. Larvae are present in April in colonies from the Abrolhos (WAM 367.80) and from Rottnest I. (> *P. gelatinosa* Kott, 1957a). The larval trunk is about 2mm long, with a large part of that length (about two-thirds) anterior to the oozooid taken up by a yolk mass. The short thick stalks of the 3 (triradially arranged) adhesive organs are not expanded into ectodermal ampullae. The central protrusion of each adhesive organ is rather narrow and cylindrical.

REMARKS. The relatively numerous rows of stigmata, longitudinal muscles on the thorax, and longitudinal stomach folds, as well as the larvae and the pigmentation of the zooids distinguish this species from *Polycitor giganteus* which has a similar bulky, and firm gelatinous colony and a similar long branchial sac that narrows towards its posterior end. The long yolk-filled anterior part of the larval trunk is unique. The abdominal brooding of the larvae and triradial arrangement of adhesive organs was also observed by Millar (1963a and 1975), and occurs also in *P. annulus* n.sp. from Heron I. (see above).

In preservative the colonies sometimes resemble those of *Sigillina grandissima*, especially since the zooids are the same dark colour. The latter species is distinguished by its long vascular stolon, relatively short oesophagus, smooth stomach and more conspicuous transverse muscles. *Eudistoma superlatum* n.sp. also forms massive but lobed colonies, and has a long vascular stolon (unlike the present species).

Millar (1975) assigned 3 colonies — 2 from the Philippines and one from the Kei Is — to this species. They are all small finger- or club-shaped lobes, joined basally, and are not the large gelatinous cushions of the present material. Therefore only the Marongas specimen 20.3.1914 (which has the characteristic larva) can be positively assigned to this species. The specimen from the Kei Is resembles *Clavelina arafurensis* in the proportion of oblique to longitudinal muscles, although the orange vesicles in the test reported by Millar have not been recorded for *C. arafurensis*. One colony from the Philippines (ZMC 20.iii.14) may be a colony of *Polycitor translucidus*, with characteristically long zooids and parallel longitudinal thoracic muscles.

Specimens from New Caledonia (Monniot 1988) have a smaller than usual larval trunk (1.6mm long).

Polycitor emergens n.sp.
(Fig. 63)

DISTRIBUTION

TYPE LOCALITY: New South Wales (off Cronulla, 60m, coll. J. McIntyre 17.6.65, holotype AM Y1124, paratypes AM Y837).

FURTHER RECORDS: None.

DESCRIPTION:

EXTERNAL APPEARANCE: Colonies consist of upright cylindrical finger-like lobes arising from a common basal mass of test concealed by an almost spherical mass of sand. The sand can be removed to show the basal mass of test subdivided into irregular branches covered with fine, branched and rather ragged, flat, narrow, tag-like projections of the test to which the sand adheres. These act as roots holding the colony firmly in the sandy substrate. The upright, free lobes of the colony are up to 2cm long, and the basal sandy part is about 1.5cm in diameter. The test is

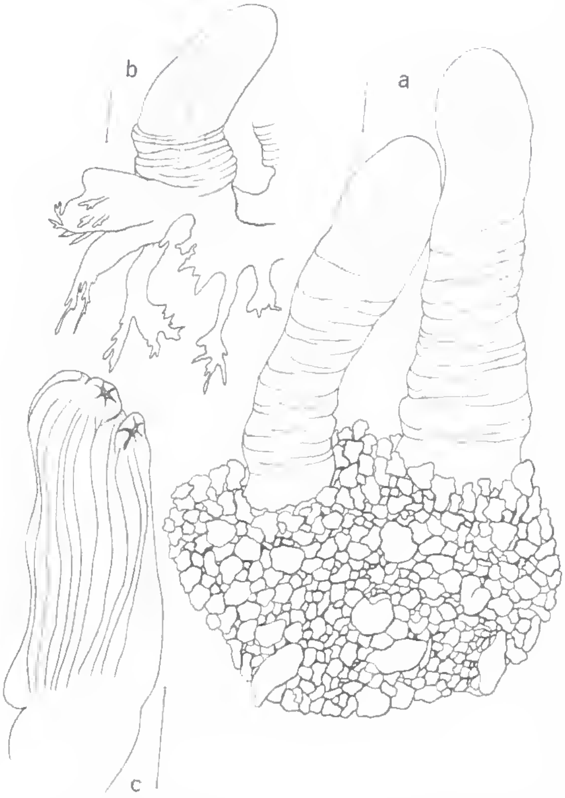


FIG. 63, *Polycitor emergens* n.sp. (paratypes AM Y837): **a**, colony; **b**, colony with sand removed from basal half showing zooids extending out into basal root-like branches; **c**, thorax. Scales: **a**,**b**, 2mm; **c**, 0.5mm.

translucent and relatively soft on the upper free ends of the cylindrical lobes, but becomes tougher toward the base, where the surface layer is transversely wrinkled and opaque. The basal sand-covered part of the test is tough.

Zooids are parallel to one another and open to the surface on the top of each upright lobe where the test is particularly delicate. They are long, and the posterior ends of from one to 3 or more extend out into each branch of the basal part of the colony.

INTERNAL STRUCTURE: Zooids are contracted in both the holotype and two paratype colonies. Both apertures are anterior, each with 6 well-defined lobes. Nine or 10 strong parallel longitudinal muscles have the formula 6B,2D,2A. They extend in 2 broad bands along the ventral part of the abdomen. The internal layer of circular muscles is inconspicuous, dorsal languets are triangular with a long point, and there are 8 rows of stigmata with about 20 per row.

The usual long oesophagus opens into the smooth stomach in the posterior third of the abdomen. The anal opening is bilabiate. Gonads, present in the gut loop, have relatively small pyriform male follicles.

REMARKS: The tendency for the basal part of the colony to break up into branches into which the posterior ends of the zooids project has been recorded only in this genus — in the present species and in *Polycitor subarborensis* (see below). The present species can be distinguished by its small, upright, cylindrical colony lobes, and its irregular basal branches, each containing the posterior part of several zooids. Only the tips of the sandy basal branches of *P. subarborensis* are produced into the fine and sometimes relatively long branching root-like tags produced from the test. In the present species these occur all over the basal test and hold the thick coat of sand around the base of the colony. Zooids of *P. subarborensis* also have more numerous muscles than the present species.

Basal stolons of certain clavelinid and pycnoclavellid colonies which support separate zooids are not homologous or even analogous with the basal branches of these *Polycitor* colonies in which the upper parts of the zooids are entirely embedded. Basal branches of both the present species and *P. subarborensis* appear, at least functionally, analagous to the basal root-like processes of stolidobranch ascidians, by which they are attached to or are rooted in the substrate. However, they are not homologous. The present colonies are unusual in that the projections by which they are anchored contain the posterior ends of the zooids and are not merely solid outgrowths of the test. Zooids of *P. subarborensis* and the present species project to the end of the basal branches of the colony. Thus these basal branches seem homologous with basal parts of colonies of other species in the genus, and probably are the result of subdivision separating the posterior ends of the zooids from one another, rather than simple outgrowths of the test.

It is the form of the colony and its tough test that distinguishes the species from *Polycitor translucidus* which has similar long, but narrow, zooids with only about 8 rows of stigmata and a smooth stomach.

Polycitor giganteus (Herdman, 1899)
(Fig. 64, Plate 13d-h)

Polyclinum giganteum Herdman, 1899, p. 79.
Polycitor giganteus: Kott, 1957a, p. 83; 1972a, p. 9; 1972b, p. 171; 1972d, p. 244; 1975, p. 2; 1976, p. 57. Millar, 1963a, p. 709. **Not** Sluiter, 1919, p. 10.
Polyclinum globosum Herdman, 1899, p. 80.
Polycitor gelatinosa Kott, 1957a, p. 83 (part, specimens from South Australia).

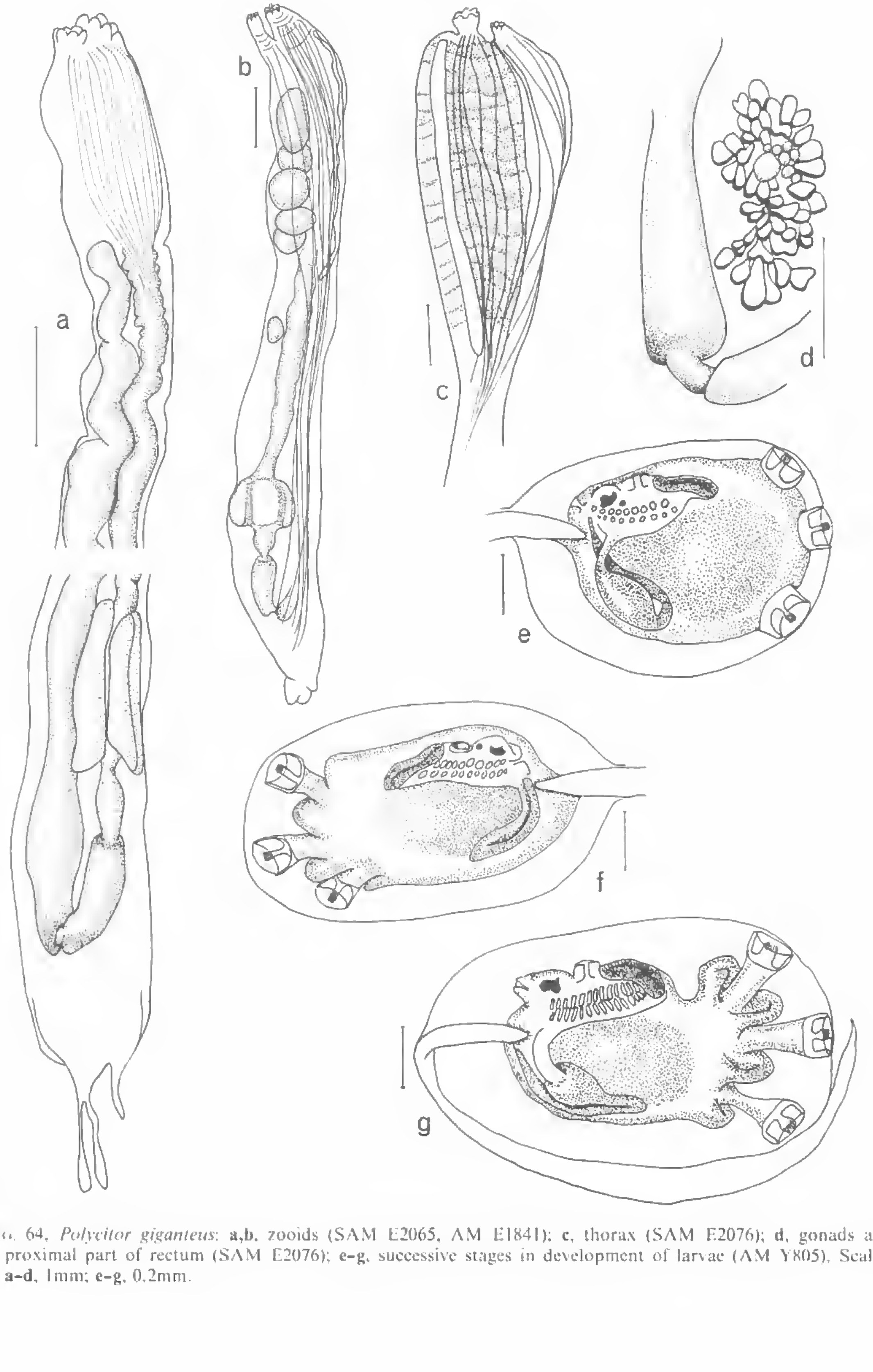


FIG. 64, *Polycitor giganteus*: **a,b**, zooids (SAM E2065, AM E1841); **c**, thorax (SAM E2076); **d**, gonads and proximal part of rectum (SAM E2076); **e–g**, successive stages in development of larvae (AM Y805). Scales, **a–d**, 1mm; **e–g**, 0.2mm.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 1038.83; Shark Bay, WAM 821.83 *QM GH2141*). South Australia (Great Australian Bight, SAM E2067, QM GH925 GH931 GH1291 GH2318 GH2386 GH2388; Spencer Gulf, SAM E2060-2 E2068, QM GH4853; Nuyts Archipelago, SAM E2063-4, QM GH2306; Yorke Peninsula, SAM E2066, QM GH2373; St Vincent Gulf, SAM E2065, QM G9314; Kangaroo I., SAM E2069, QM G11990). Tasmania (Flinders I. QM GH1291; Oyster Bay, AM U358). Victoria (Ninety Mile Beach QM G11862; Bass Strait, MV; Gabo I., QM G9478). New South Wales (Bermagui, AM Y2194; Jervis Bay, QM G10021-4; Port Stephens, AM Y2000; Botany Bay, QM G10164; Clarence River mouth, AM E1841; Arrawarra, GH4357; Solitary I., QM G9635; Lord Howe I., QM GH4376). Queensland (Mooloolabah, QM GH4324).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — SAM E2072 E2075-6 Kott 1972b 1976; St. Vincent Gulf — AM Y1304 *P. gelatinosa*: Kott, 1957a, SAM D239 E2071 E2074 Kott 1972a; Investigator Strait — Kott 1972b; West I. — Kott 1972a 1975). Victoria (Lakes Entrance — AM Y1130 Y1312 Kott 1957a; Port Phillip Bay — AM Y1295 Kott 1957a 1976, Millar 1963a; Western Port — AM Y1293 Kott 1976; Mallacoota Inlet — Kott 1976). New South Wales (Jervis Bay, Port Jackson — AM Y3930 U3934 Herdman 1899, AM Y1294 Y1305 Y1308 Kott 1957a, Millar 1963a; Botany Bay — AM Y805 Y808 Y810 Y831 Kott 1972d).

The species is common in shallower waters (subtidal to 24m) from southern Australia to Port Jackson (NSW), but has also been taken down to 400m off the NSW coast off Bermagui (AM Y2194). It appears an Australian indigenous species recorded most commonly around the south-eastern half of the continent.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are massive, up to 12cm in diameter. They are spherical to top-shaped, fixed by a part of the undersurface which usually forms a short, thick stump that just elevates the colony above the substrate. The test is always firm and gelatinous, and completely transparent and glassy to cloudy and translucent. Zooids usually open around the sides and upper surface of the colony, although occasionally in relatively small colonies, zooid openings are confined to the upper surface. Zooids converge from the surface in toward the centre of the base of the colony. In preserved colonies they are invariably found contracted and withdrawn from the surface. The zooid openings are arranged evenly on the surface of the colony but their posterior ends cross one another when they are withdrawn from the surface. Zooids are not in systems. In living colonies the test is usually glassy and transparent, and zooids are either bright orange or white and can be seen as white or yellow streaks radiating out from the centre of the transparent colonies. In preservative zooids are either white or pinkish, however, there is no correlation between living and preserved colours — colonies reported by the collectors to have had bright orange zooids are either pinkish or white in preservative, as are zooids reported to be white when living.

INTERNAL STRUCTURE: Zooids are robust and long, even in a contracted state they can measure to 1cm, and in life are much longer. They have 6 well defined lobes around each aperture. The body musculature is strong, consisting of 12 longitudinal thoracic bands on each side which continue along the length of the abdomen as two wide ventral bands of muscle. Thoracic bands extend from the branchial siphon, from the space between the siphons, and from the other siphon according to the formula 6B,3D,3A. None of the longitudinal muscle bands cross the endostyle. The transverse or circular musculature is usually inconspicuous, except for the sphincter muscles around each siphon. The transverse wrinkles of the ectodermal layer of the body wall resulting from contraction of the thoracic muscles can be mistaken for transverse muscles on superficial examination of the zooids. The neural complex is large and the opening of the neural gland is a simple circular opening directed forwards. Six large but rather stumpy branchial tentacles alternate with shorter ones. Dorsal languets on the dorsal sinus are long and pointed. There are 12 to 16 rows of long rectangular stigmata, invariably found contracted. In a large specimen from Bass Strait there are 16 rows on the right and an additional half-row that does not reach the dorsal line on the left. Although often difficult to count, there appear to be between 30 and 40 stigmata in all rows except the posterior ones. In one relaxed specimen (SAM E2076) there are 40 in the anterior and 20 in the posterior rows. Parastigmatic vessels are absent.

The oesophagus is long, opening into the elongate stomach near the posterior end of the abdomen. The stomach wall has 4 grooves, and when collapsed it forms 4 pronounced folds. The posterior stomach, about the same length as the stomach, and separated from it by a short duodenal area, opens into the rectum in the pole of the gut loop. The anal border is bilabiate. Gonads, consisting of numerous male follicles and a small ovary, are contained in the posterior end of the gut loop behind the stomach at the posterior end of the abdomen. There are 2 or 3 short vascular appendages.

Embryos occur in specimens taken from South Australian waters in September (QM GH4853) and October (SAM E2075) but not in February or May. In November they are in specimens from Port Phillip, Bass Strait (MV) and Botany Bay (AM Y816). However, they are present also in June in Botany Bay (AM Y805), October at Lord Howe I. (QM GH4376), and January at Lakes Entrance and Rottnest I. (AM Y1310). Thus records suggest sexual reproduction may occur throughout the year. Ova probably are fertilised in the atrial cavity, where up to 12 eggs and embryos at various stages of development occur. The larval trunk is 1.4mm long, and the tail is wound half to three quarters of the way around it.

Single median ampullae are in the anterior mid-line dorsal and ventral to and alternating with the stalked adhesive organs. Ampullae subsequently become bilobed. In mature larvae they often appear as paired lobes. An otolith and ocellus are in the cerebral vesicle, and a large mass of yolk in the centre of the larval trunk. The protruding part of each adhesive organ is rather narrow and cylindrical.

Remarks: Preserved colonies of this species are readily confused with *Polycitor circes* which also has large gelatinous colonies, and zooids with a long thorax decreasing in width posteriorly. However, the zooids of *P. circes* have more numerous longitudinal muscle bands, rows of stigmata and stomach folds.

Kott's (1976) suggestion that the orange in certain colonies occurs when the zooids are not withdrawn from the surface was not confirmed in the present study although eggs and larvae of both white and orange zooids contain the same orange pigment in the yolk. Orange zooids also have pigment in the body wall, and it is absent from the white zooids. Apparently there are two colour phases of this species. The great range in numbers of rows of stigmata referred to by Kott (1957a *et seq.*) probably results from difficulties in counting these in contracted zooids.

Polycitor nubilus n.sp.

(Fig. 65a,b. Plate 13i)

Distribution

Type Locality: South Australia (Investigator Group, Flinders I., Lighthouse Point in caves and overhangs 8m, coll. N. Holmes, photo index PE0071/R969, holotype SAM E2079).

Further Records: None.

Description

External Appearance: The holotype colony is the only specimen available. It has an almost spherical head about 4cm in diameter and a short thick stalk about half the diameter of the head.

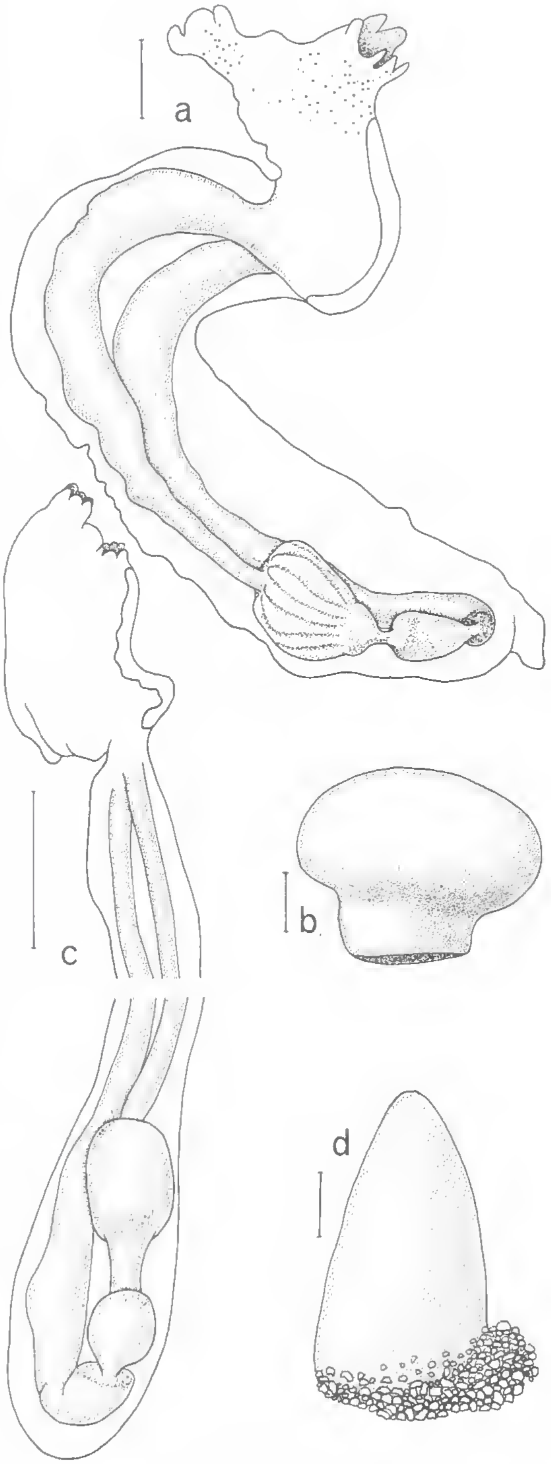


Fig. 65, *Polycitor nubilus* n.sp. (holotype SAM 2079): **a**, zooid; **b**, colony outline. *Polycitor obeliscus* (holotype MV H167): **c**, zooid; **d**, colony outline. Scales: **a**, 0.5mm; **b,d**, 1cm; **c**, 1mm.

Zooids are relatively crowded, opening all around the head. In life the colony is a cloudy, cream colour, with translucent circular areas over each zooid, separated from one another by narrow bands of opaque test. In preservative the test of the head is gelatinous, translucent and a slightly rosy colour.

Internal Structure: Zooids are dark in preservative, with pigment particles scattered in the body wall, especially around the anterior end. Zooids are muscular, and contracted. Each of the apertures is deeply divided into 6 pointed or rounded lobes. Longitudinal thoracic muscles from the siphons and the intersiphonal interval have the formula 6B,3D,3A. They continue along the abdomen as two wide ventral bands and terminate at the posterior end of the zooid. Transverse muscles are inconspicuous. Twelve fairly long tentacles in a posterior circle alternate with 12 shorter ones in a second circle. Small, irregularly spaced tentacles are in an anterior circle. The simple opening of the neural gland is directed anteriorly. There are 11 rows of about 20 rectangular stigmata.

The long oesophagus opens into the stomach in the posterior quarter of the abdomen. The stomach wall has 15 parallel, longitudinal folds. An oval posterior stomach is constricted off from the rectum in the pole of the gut loop. Gonads are present in the gut loop. There is a short, branched vascular extension from the posterior end of the body.

Remarks: Although photographs of the living specimen do not show the zooids pigmented, the dark pigmentation of the preserved specimens is conspicuous and distinctive. Unlike *Polycitor annulus* n.sp., which has darkly pigmented living zooids as well as preserved ones, the pigment particles are not in longitudinal lines down the thorax in the present species but are scattered rather evenly in the body wall, becoming more crowded anteriorly. Branchial sacs are similar in the two species. In addition to the arrangement of the pigment particles in preserved specimens, *P. annulus* n.sp. differs from the present species in having a clear transparent test and more numerous (18) longitudinal muscle bands. Of the other *Polycitor* spp. with a folded stomach, *P. calamus* n.sp. is distinguished by its colour and long cylindrical stalk, *P. circes* has more numerous longitudinal thoracic muscles and rows of stigmata, and *P. cerasus* n.sp. has conspicuous circular thoracic muscles as well as the longitudinal ones. The larva of the present new species is not known.

Polycitor obeliscus Kott, 1972

(Fig. 65c,d)

Polycitor obeliscum Kott, 1972b, p. 171.

Distribution

New Records: None.

Previously Recorded: South Australia (Investigator Strait holotype MV H167).

Description

External Appearance: The holotype is the only colony available. The colony is an upright cone 5cm high and about 2.5cm in diameter around the base. It is firm, with sand throughout the internal test. Sand is also in the surface test around the base of the colony, but absent from the surface test of the upper part. Zooids open all over the upper surface of the colony, and they converge inwards at an angle to the surface. Between sand grains the test is firm and translucent.

Internal Structure: Zooids are about 9mm long but are contracted. The thorax has an almost continuous coat of outer longitudinal muscle bands overlying the layer of circular ones. The longitudinal muscles continue along the length of the abdomen in 2 wide bands.

There are 6 rows of about 12 stigmata. However, stigmata are hard to count owing to the contraction of the thorax — and it is possible there are more. The oesophageal necks of the zooids are particularly long. An almost spherical, relatively short and smooth-walled stomach, an expanded duodenal area and a short rounded posterior stomach are in the descending limb of the gut loop at the posterior end of the abdomen. Mature gonads are not present in these zooids (collected in January). The larvae are not known.

Remarks: The species is unusual in *Polycitor* in having embedded sand, and relatively few rows of stigmata. The zooid, muscular, and thus resembling *P. circes*, is readily distinguished from it by the smooth stomach and embedded sand.

Polycitor subarborensis Kott, 1957

(Fig. 66a c)

Polycitor subarborensis Kott, 1957a, p. 81.

Distribution

New Records: None.

Previously Recorded: New South Wales (Ulladulla, AM Y1298 holotype)

Description

External Appearance: The colony is a small, more or less dome-shaped, glassy, transparent, sessile cushion about 1cm in diameter but only about 0.5cm high, with 9 or 10 cylindrical, sand-covered root-like structures about 1cm long

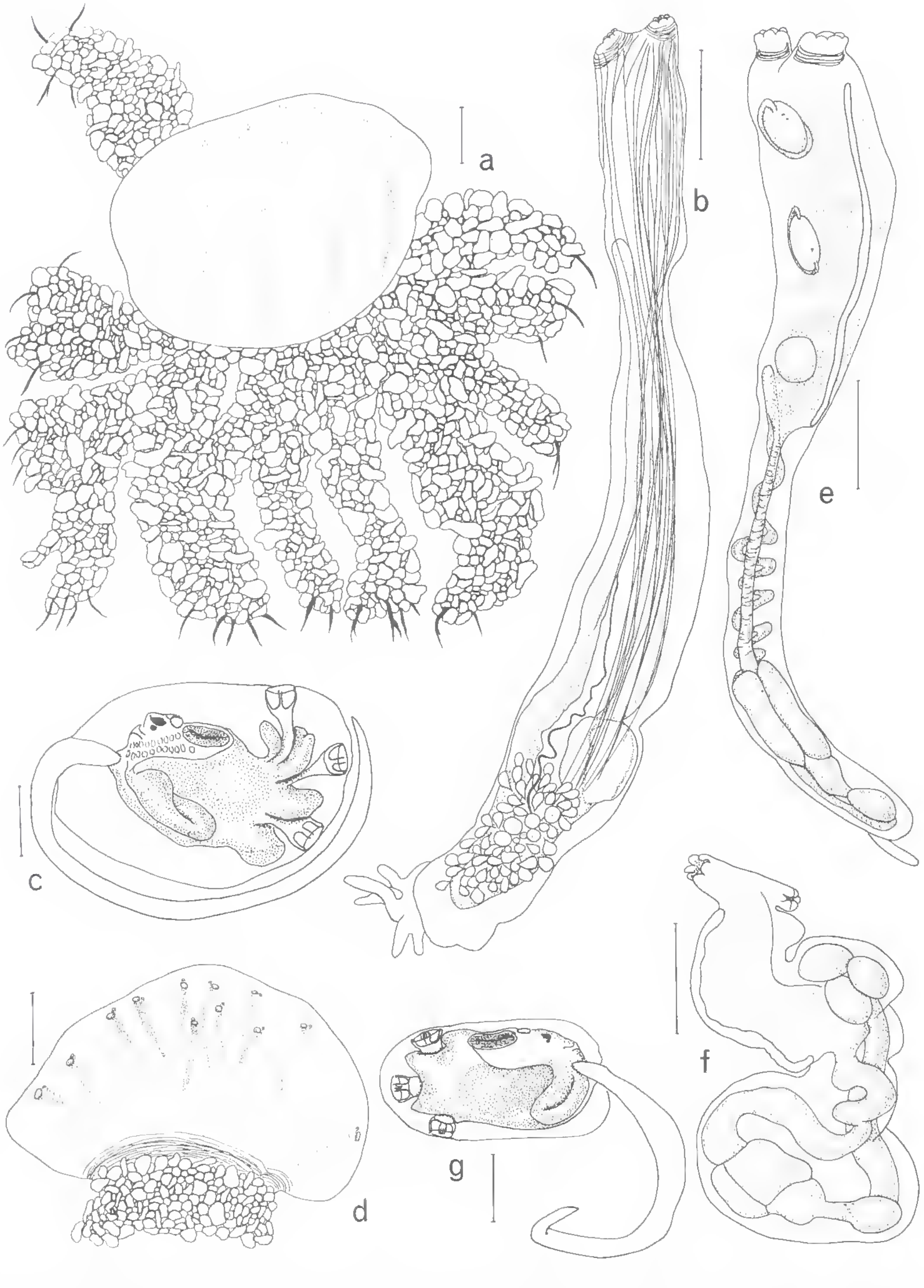


FIG. 66, *Polycitor subarborensis* (holotype AM Y1298): **a**, colony; **b**, zooid, **c**, larva. *Polycitor translucidus*: **d**, colony (QM G4332); **e**, zooid with embryos (QM GH4345); **f**, much contracted zooid with embryos (QM GH4343); **g,** larva (QM GH4325). Scales: **a,** 2mm; **b,e,f,** 1mm; **c,g,** 0.2mm; **d,** 5mm.

projecting down and out from the under surface of the glassy dome. Occasionally they branch once along their length. The sand is embedded in their surface test. Zooids open on the upper glassy surface of the colony and project down into the sandy root-like branches, each terminal branch containing the posterior end of one zooid. The terminal ends of these branches also have some rather short irregular test processes to which additional sand adheres. An irregular knob of zooid-free test growing from the upper surface may be an abnormality.

INTERNAL STRUCTURE: Zooids are withdrawn from the upper surface in this contracted colony. Both apertures are anterior, with a sphincter around the base of each short, 6-lobed siphon. Longitudinal muscles are numerous, arranged on the thorax according to the formula 12B,2D,2A. The 6 most ventral muscles lie fairly close to one another, crowded together along each side of the endostyle. Transverse muscles are inconspicuous.

On the abdomen, the muscles form 2 or 3 exceptionally wide bands leave only the dorsal border muscle-free. There are 8 rows of about 20 stigmata. The oesophagus is, as usual, long, opening into the smooth-walled stomach in the posterior end of the abdomen. Gonads are large, with short, lobed, pyriform male follicles and about 12 eggs in the ovary.

The holotype colony, which was collected in January, has single embryos near the surface of the head, although none in the zooids themselves. These embryos may have been ejected by the zooid as it contracted and withdrew from the surface while being collected. The larval trunk is moderately large (1mm long), with a thick, tough test. The tail reaches the anterior end of the trunk. Three median adhesive organs alternate with ampullae. These ampullae are single and median in the immature larvae, but they subsequently subdivide into paired lobes, as in the larvae of *Polycitor giganteus*. The central protrusion of the adhesive organs is narrow and cylindrical.

REMARKS: Both larvae and zooids (with 8 rows of stigmata and the smooth-walled stomach that may collapse into 4 folds) are similar to those of *P. translucidus*. However, the present species has more longitudinal thoracic muscles, and the division of the basal half of the colony into sandy root-like process is an almost unique feature, shared only with *P. emergens* n.sp. (see above).

Polycitor translucidus Kott, 1957
(Fig. 66d–g)

Polycitor translucida Kott, 1957a, p. 81. Monniot and Monniot 1987, p. 70; Monniot, 1988, p. 209.
Polycitor circes: Millar 1975, p. 205 (part, specimen from the Philippines ZMC 19.iii.41).
? *P. crystallinus*: Monniot, 1988, p. 209.

DISTRIBUTION

NEW RECORDS: Western Australia (Shark Bay, WAM 82.83 1041.83; Cockburn Sound, WAM 1034.83). Victoria (Wilson's Promontory, MV F54184). Queensland (Maroochydore, QM GH4329 GH4358; Wistari Reef, QM GH4333 GH4339 GH4436; Heron I., QM G10010 GH4325-32 GH4334-8 GH4340-5 GH4368 GH4370 GH4583).

PREVIOUSLY RECORDED: Western Australia (Rottnest I. — Kott 1957a). French Polynesia (Monniot and Monniot 1987). Philippines (Millar 1975). New Caledonia (Monniot 1988).

The few records of this species, other than from Heron I. where collecting effort has been greater than elsewhere, may be because of its cryptic habit and its completely transparent glassy test. Its recorded range suggests a West Pacific species probably with the usual wide geographic range of that fauna (see Kott 1985).

DESCRIPTION

EXTERNAL APPEARANCE: This beautiful species has a wedge-, mushroom-, top-shaped to upright almost cylindrical colony tucked into small crevices from which its upper surface protrudes. The narrow upright colonies, in which the head is not expanded and the number of zooids are fewer are apparently younger than the others. Colonies are up to 2cm in diameter on their upper surface — which may be flattened or rounded, and about 1.5cm high. They are fixed by a short stalk often separated from the expanded head by a slight constriction. Zooids extend down into the base of the stalk. The test of the head is absolutely clear and glassy and the zooid openings show on the surface as fine white rings that disappear as the zooids withdraw from the surface when they are disturbed.

In life the thoraces of the zooids are 'buff yellow', 'salmon buff', 'maize yellow', to 'deep chrome' (Ridgeway 1886). The stomach is usually 'cadmium orange' and developing embryos are also orange. In preservative they are cream to pink.

INTERNAL STRUCTURE: Zooids, when partially relaxed, are about 7mm long. They have 6 rounded lobes around each aperture, and a shallow band of circular muscle fibres around the base of each short siphon. Nine to 12 well separated, longitudinal muscle bands on the thorax have the formula 6–8B,1D,2–4A. These continue along the abdomen in the usual 2 wide ventral bands. Twelve rather long tentacles alternate with small almost rudimentary ones. Dorsal languets are long and pointed. There are 8 to 10 rows of about 20 to 30 stigmata. The larger colonies (MV F54184, WAM 1041.83) have the maximum numbers of longitudinal muscle bands and stigmata.

The oesophagus is long but usually wrinkled, while the rectum is bent, undulating and folded in the fixed specimens — which, even though narcotised, and with the thorax relaxed, always have a contracted abdomen. The stomach, in the posterior end of the abdomen has a suture line, but apparently no folds. There is an oval posterior stomach and a constriction in the pole of the gut loop separates it from the rectum. The anal border at the posterior end of the atrial cavity is bilabiate.

Gonads with small pyriform sometimes bilobed male follicles are in the gut loop, posterior to the stomach. Larvae probably are fertilised and complete their development in the posterior part of the atrial cavity, where up to 6 embryos are crowded. Larvae are in colonies collected in May, July, August and November, but not in colonies collected between January and March — the hottest time of the year at Heron I. where diurnal temperature variations in the intertidal area are high.

Larvae are small, with a trunk 0.6 to 0.8mm long. The tail is wound half to three-quarters of the distance around the trunk. The 3 adhesive organs, on narrow stalks, alternate with conical ectodermal ampullae in the median line. The central protrusion of the adhesive organs is narrow and cylindrical.

Remarks: One of the principal characteristics of this species is the small size and simplicity of its zooids (which probably is a result of its small size), *viz.* relatively few rows of stigmata and muscle bands, a smooth stomach (rather than one with folds), and small larvae. The colour of the living specimens resembles the range found in *Polycitor giganteus*, although the test is clearer and more glassy in the present species.

Specimens from New Caledonia assigned to the Mediterranean *P. crystallinus* by Monniot (1988) may be synonyms of the present species although their colonies are larger than usual. Both zooids and larvae are similar, and it is possible the colonies increase in size with age, and in sublittoral habitats.

Genus **Cystodytes** Drasche, 1884

Type species: *Distoma dellachiajei* Della Valle, 1877.

The genus is characterised by the presence of a capsule formed of layers of overlapping saucer-shaped calcareous spicules that encases the abdomen of each zooid, and into which the whole zooid sometimes withdraws when it contracts. The cavity in the firm, gelatinous and translucent test in which the zooids are contained is hourglass-shaped — the thoracic and abdominal compartments being partially separated by a constriction of the test with a circular constrictor muscle embedded in it. This circular muscle is connected to the zooid around the top of the oesophageal neck. The strong musculature consists of a thoracic meshwork of longitudinal and transverse bands, with the longitudinal muscles continuing onto the abdomen as a pair of wide bands, one on each side of the mid-ventral line. There are 4 rows of stigmata without parastigmatic vessels. The shield-shaped stomach is smooth, in the posterior half of the abdomen. Gonads, consisting of a circular arrangement of club-shaped testis follicles converging toward the vas deferens at the centre of the circle, and an ovary containing one egg, are in the gut loop. Zooids, usually in circles with the atrial apertures in the centre of the circle, form rudimentary systems as in *Eudistoma* and *Polycitorella*.

A single large embryo incubates in the brood pouch, which is constricted off from the body wall at the top of the abdomen. The egg apparently is fertilised at the base of the oviduct. As it increases in size and moves up the body it projects from the side of the abdomen and becomes more constricted from it.

The larva has primarily 3 stalked adhesive organs in the anterior mid-line surrounded by a circular fold of the larval ectoderm. As the larva matures, long radial grooves develop between the base of this fold and its anterior edge. Subsequently the grooves perforate leaving, embedded in the test around the adhesive organs, a ring of ectoderm attached by strands to the main part of the larval trunk. This unusual apparatus is homologous with the ectodermal ampullae of other forms. Instead of separate external ampullae projecting from around the anterior end of the trunk, a continuous ring of ectoderm projects forwards.

Adhesive organs have a large conical central protrusion with the same bulbous appearance as the central cone of the adhesive organs in *Distaplia* (see Cloney 1977), and differing from the more or less cylindrical, flat-topped, central protrusion generally found in the adhesive organs of the Polycitoridae. There also are 4 rows of stigmata in the oozooid like *Distaplia*.

Despite this resemblance to larvae of *Distaplia*, the relationships of the genus appear with *Polycitorella*, which also has particularly muscular zooids, a constrictor muscle embedded in the test around the top of the oesophageal neck, calcareous spicules, and a single embryo brooded at the top of the abdomen.

Cystodytes may be more diverse than is known at present. However, although several species have been described, their distinctions from the apparently wide-ranging species *Cystodytes dellachiajei* are not satisfactory. As could be expected for such a wide-ranging species, the recorded specimens demonstrate a deal of diversity reflected in the pigmentation and size of the colonies. Although at this stage the diversity in specimens assigned to this species is attributed to intraspecific variations, it is possible that genetic studies could establish patterns that result from speciation. Zooids are remarkably uniform, although their strong musculature does allow for a degree of flexibility in their superficial appearance.

Cystodytes dellachiajei (Della Valle, 1877)
(Fig. 67. Plate 14a-d)

? *Aplidium lobatum* Della Chiajei, 1841, p. 30.
Distoma dellachiajei Della Valle, 1877, p. 40.
Cystodytes dellachiajei: Hartmeyer, 1912, p. 171. Michaelsen, 1915, p. 483; 1923, p.28; 1930, p. 501. Harant, 1929, p. 41. Van Name, 1945, p. 133. Brewin, 1948, p. 119; 1951, p. 104; 1952a, p. 452; 1956c, p. 122; 1958, p. 44; 1960, p. 119. Kott, 1954, p. 154; 1972a, p. 11; 1972b, p. 172; 1981, p. 154. Tokioka, 1950, p. 120. Millar, 1953b, p. 284; 1960, p. 82; 1962, p. 143; 1963a, p. 713; 1964, p. 166; 1966a, p. 365; 1978, p. 100; 1982, p. 15.
Cystodytes dellachiaiae: Van Name, 1921, p. 360. Berrill, 1932, p. 78. Kott, 1957a, p. 68.
Cystodytes Della Chiajei: Pérès, 1948, p. 17.
Cystodytes durus Drasche, 1883, p. 13.
Cystodytes cretaceous Drasche, 1883, p. 18.
Cystodytes draschii Herdman, 1886, p. 137. Van Name, 1902, p. 347. Michaelsen, 1915, p. 484 (draschei); 1924, 1924, p. 286 (draschei).
Cystodytes philippinensis Herdman, 1886, p. 140; 1891, p. 615. Sluiter, 1909, p. 28. Caullery, 1909, p. 45. Hartmeyer, 1909, p. 1434. Van Name, 1918, p. 138.
Cystodytes aucklandicus Nott, 1892, p. 323.
Cystodytes perspicuus Nott, 1892, p. 326.
Cystodytes violaceus Van Name, 1902, p. 348. Harant, 1925, p. 3.
Cystodytes ceylonensis Herdman, 1906, p. 334.
Cystodytes hapu Monniot and Monniot, 1987, p. 64.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 1013.83; Recherche Archipelago, WAM 149.75; Shark Bay, WAM 827.83; Cervantes Reef, WAM 194.87; Houtmans' Abrolhos, WAM 386.75 825.83 200.88 204.88; Dongara WAM 1011 2.83; Cockburn Sound, WAM 8.75 865.82 817.83 919.83 1010.83). South Australia (Great Australian Bight, QM GH2382; Spencer Gulf, QM GH4404; St Vincent Gulf, QM GH2401–2). Tasmania (d'Entrecasteaux Channel QM GH9996). Victoria (Portsea, QM G11922). New South Wales (Jervis Bay, QM G10019). Queensland (Capricorn Group, QM G9481 G9596 G9890–3 G9895 G9897–9 G9901–7 G9922 G10017–8 G10033 GH3478–9 GH3816 GH4383–4 GH4412 8 GH4443–6 GH4476; Lizard I, GH3118 GH3826).

PREVIOUSLY RECORDED: Western Australia (Dampier Archipelago — Millar 1963a; Shark Bay — Michaelsen 1930; Cockburn Sound — Michaelsen 1930, Kott 1957a; Albany — Kott 1954 1957a). South Australia (Great Australian Bight — Kott 1972b; St. Vincent Gulf — Kott 1972a). Tasmania (Maria I. — Kott 1954). Victoria (Port Phillip Bay — Millar 1966a; Barwon Heads — Millar 1966a). New Zealand (North, South and Chatham Is — Nott 1892, Michaelsen 1924, Brewin 1948 1951 1952a 1956c 1958, Millar 1960 1982). New Caledonia (Monniot 1988). Palau Is (Tokioka 1950). Philippines (Herdman 1886, Sluiter 1909, Van Name 1918). Fiji (Kott 1981). Tahiti (Monniot and Monniot 1987). Sri Lanka (Herdman 1906). West Indian Ocean (Mozambique — Millar 1962). Mediterranean (Della Valle 1877, Drasche 1883, Harant 1925 1929). Eastern Atlantic (West Africa — Michaelsen 1915, Millar 1953b, Pérès 1948, Canary Is — Hartmeyer 1912; Azores — Michaelsen 1923). Western Atlantic (Bermuda — Van Name 1902; Brazil — Herdman 1886; Millar 1978; Patagonian Shelf — Millar 1960; Virgin Is — Van Name 1902). Eastern Pacific (California — Van Name 1902).

The species is not confined to the tropics. It extends around the temperate coast of Australia, and south to the Patagonian region in the eastern Pacific. In the Atlantic it extends north to the Azores and Canary Is. There are two surprising gaps in the recorded range — the species is not known from either the western Pacific north of the Philippines, or from South Africa. It could be expected to occur in those locations. The species also has a wide depth range, from the intertidal zone down to 736m (off Brazil: Herdman 1886).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are cushion-shaped to large investing sheets of translucent, firm, gelatinous test, through which patches of white — the capsules of saucer-shaped calcareous spicules up to 0.8mm in diameter — can be detected. In one colony from South Australia (QM GH2382) small spheroidal spicules in the test surround the top of each of the capsules. Living colonies that are white, through pink to purple ('auricular purple': Ridgeway 1886) become glassy and transparent to pinkish-brown, and cloudy pink in alcohol preservative. Those grey-black, red-brown and 'dragon's blood red' (Ridgeway 1886) when living, are grey-greenish-black in preservative. Morphological differences are not associated with the different colours (see Remarks, below).

Zooids are evenly spaced, in circles of 4 to 8, with their atrial apertures in the centre of the circle. This arrangement is not easy to see in most contracted, preserved colonies, especially as the zooids usually are withdrawn away from the

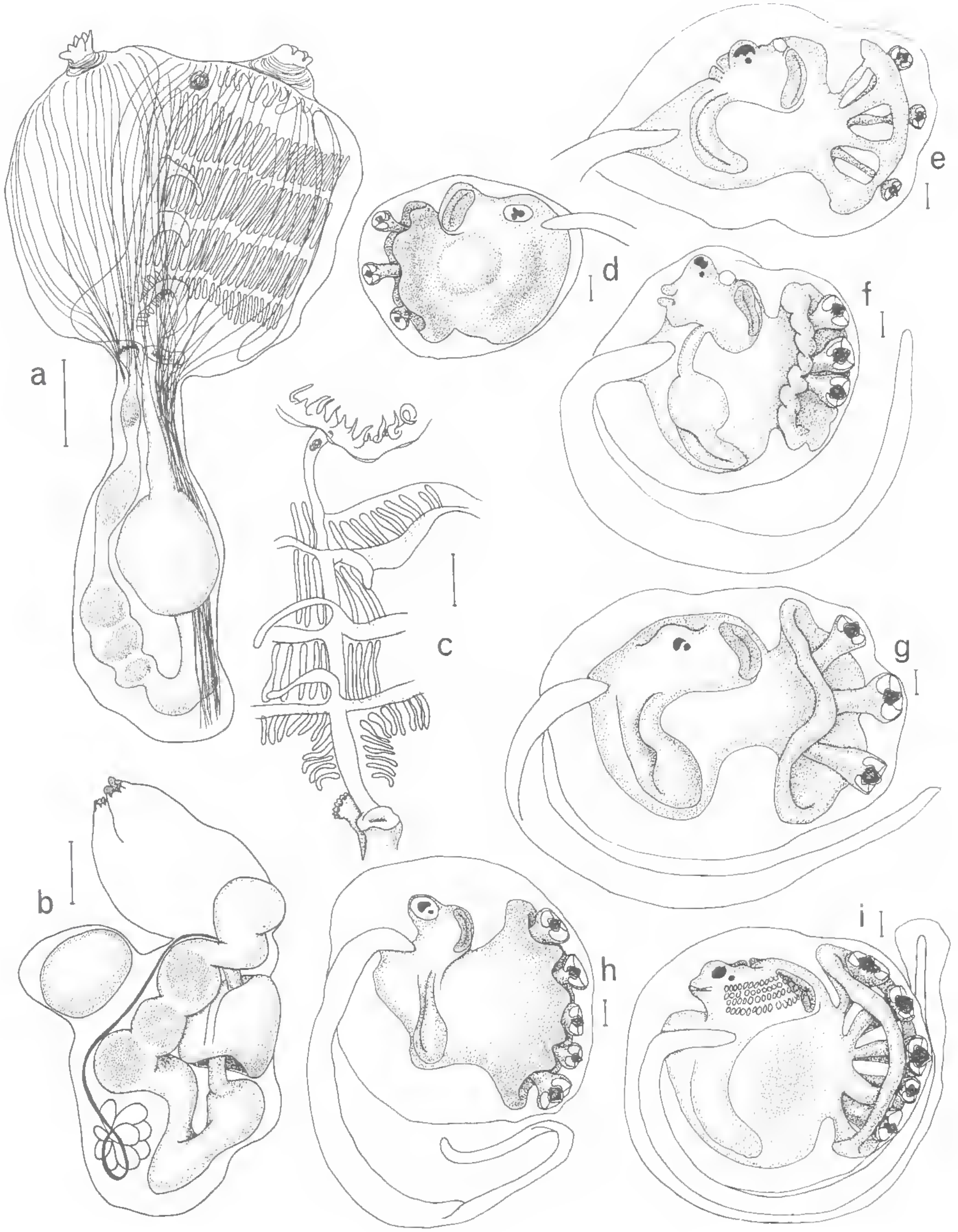


FIG. 67, *Cystodytes dellachiajei*: **a**, zooid partially relaxed (QM GH4413); **b**, zooid contracted, egg half way up abdomen (QM G9902); **c**, dorsal part of pharynx, showing last row of stigmata on each side turning posteriorly along the mid-dorsal line (QM GH4413); **d**, immature larvae (QM G5478); **e**, maturing larva (QM GH3826); **f,g**, large embryos before perforation of ampullary fold (WAM 165.75); **h,i**, larvae with 5 adhesive organs before and after perforation of ampullary fold (QM G9898). Scales: **a**, 0.5mm; **b,c**, 0.25mm; **d–i**, 0.1mm.

surface into the calcareous capsules in the middle to basal part of the test. The test has a smooth and even surface. Pigment particles are concentrated in the middle layer around the capsules and between the crowded bladder cells (which occur throughout the firm test). The branchial and atrial openings of the zooids are 6-lobed and do not protrude from the surface. The capsules are usually vertical, but occasionally are oblique or even recumbent. In some of the colonies (e.g. QM GH2382) the surface is depressed in the centre of each circle of zooid and forms an incipient cloacal cavity into which the atrial apertures open.

Internal Structure: Zooids are muscular, with numerous but fine longitudinal bands from each of the siphons. Those that extend from the facing sides of the siphons cross one another on the sides of the thorax. There are at least 20 longitudinal bands from each siphon, and also numerous fine transverse muscles. Sphincters are around the base of each siphon. The longitudinal muscles extend onto the abdomen as 2 wide, strong bands, one on each side of the ventral mid-line. They terminate abruptly at the posterior end of the abdomen. A circular evagination of the body wall around the top of the oesophageal neck contains the circular muscle embedded in the test. The test is constricted at this point to form the narrow canal between the thoracic and abdominal cavities.

The large number of muscles confers great flexibility in the ways these zooids contract, affecting the relationships and relative length of parts of the body including the siphons. The abdomen is especially affected, often being bent up at an angle to the thorax, and the two parallel limbs of the gut loop are often distorted away from the parallel arrangement they display in the relaxed zooids. Zooids are up to 4mm long when extended. Siphons (especially the atrial siphon) vary in length with contraction, sometimes being particularly long. Six lobes border each aperture.

Twelve branchial tentacles arise from the edge of a narrow muscular velum just anterior to and alternating with a circle of 12 more robust tentacles of equal length. The neural gland has a simple, anteriorly oriented opening lying in a narrow prebranchial area. An extensive unperforated pharyngeal area exists both anterior and posterior to the stigmata. Dorsal languets are long and pointed. There are about 25 stigmata in each of 4 rows. In one glassy, transparent colony and in a grey-black colony with relatively relaxed zooids, the fourth row of stigmata was turned posteriorly along each side of the dorsal sinus. It was not observed in all colonies and is either a variable phenomenon or obscured by contraction.

The gut loop is about the same length as the thorax. The smooth surfaced shield-shaped stomach is at least halfway down the abdomen, although this is not apparent in any but relaxed zooids. There is a short mid-intestine, but no posterior stomach. The rectum originates in the descending limb of the gut loop and the bilabiate anal opening is at the base of the atrial cavity. Each lip of the anus has about 5 small papillae along its border.

The testis consists of a dome-shaped mass of up to 18 club shaped follicles converging to the proximal end of the vas deferens in the centre of the more or less flat side of the dome on the right side of the abdomen. Occasionally a large ovum is on the right side of the gut loop. When testis follicles are not well developed, the vas deferens loops posteriorly and curves around the circumference of the ovum, when present, before extending anteriorly more or less parallel to the rectum. However, the vas deferens does not loop posteriorly when the testis follicles are mature, as the duct is stretched over the outside of the swollen follicles.

The large ovum probably is fertilised at the base of the oviduct. The embryo increases in size as it moves up toward the top of the abdomen, protruding from the body wall as it goes. As it increases in size the embryo in its brood pouch is separated from the upper part of the abdomen by an increasingly narrow constriction. Occasionally a second, but much smaller embryo in a secondary brood pouch, is separated from the primary one by a constriction (QM G9898).

In specimens from Heron I. ova are in the abdomen in July and August, and embryos in April (QM GH3478), July (QM GH3816), August (QM GH9895 GH9898) and October (QM GH4384), and also in April at Lizard I. (QM G9905). In South Australia larvae are present in March (QM GH2382). Gonads are absent from some specimens collected in March and September, although mature testes are in some collected in March and August. It is difficult to deduce the breeding pattern, despite the large number of specimens available. In the tropics there seem at least 2 breeding seasons, autumn and spring. The species is probably protandrous.

The larva is large, the trunk from 0.75mm to 1.2mm long and sometimes even deeper. There are usually 3 adhesive organs in the anterior midline. In two specimens from North West Reef, Capricorn Group, one purple and one reddish brown and another purple one from Wistari Reef

(QM G9898 G9895 GH4384) there are 4 to 7 adhesive organs. Other colonies of all colours have larvae with the usual 3 adhesive organs. These larvae all have the characteristic ectodermal ring around the adhesive organs. They have 4 rows of stigmata.

REMARKS: This species has always been poorly described, owing to the marked contraction of the strong body muscles. The zooids are difficult to narcotise, and in the newly recorded material from the Capricorn Group which were all narcotised (menthol) before fixation, only one specimen (QM GH4413) has the whole zooid, including the thorax, extended. Herdman (1886) refers to 'small' and 'not very numerous' stigmata, and 'exceptionally long and numerous' branchial tentacles (Herdman, 1886, p. 136). None of these observations could be confirmed in the course of the present study. Similarly, Van Name (1945, p. 133) incorrectly believed embryos were incubated in the atrial cavity, and the longitudinal muscles spread out over the sides of abdomen in a thin layer.

The interpretation of the colour variations in this species is a problem. The 3 most commonly occurring types are those with glassy transparent test, both living and in preservative, which usually form rather small cushions never more than 1cm in diameter; those with a deep purple or 'cinnamon rufus' or 'dragon's blood red' (Ridgeway 1886) test which form rather larger cushions up to 2cm in diameter, and are a cloudy brownish pink in preservative; and those that are grey-black both living and in preservative that sometimes form more extensive colonies. However, intermediate forms do occur — small light grey colonies, transparent pink ones, and extensive sheets of purple colony. Variations occur in the number of larval adhesive organs and in the size and shape of the larval trunk, but these cannot be correlated with any classification based on the colour or size of the colony. No other variations in zooid morphology were observed. Further, the different colour variants occur sympatrically throughout the wide range set out above. They could either be indicative of genetic diversity in this cosmopolitan species; or metabolic colours relating to habitat or diet or some combination of these factors.

The small spheroidal spicules that Tokioka (1950) used to separate *Cystodytes philippinensis* Herdman, 1886 from the present species occur also in a specimen from South Australia (QM GH2382).

Without any indication of how each is related to previously recorded material, or to one another, Monniot (F., 1988) has described 7 new species of *Cystodytes* from New Caledonia. These species have been determined on the basis of colour, the presence or absence of systems, the course of the proximal part of the vas deferens, the number of testis follicles, the numbers of siphonal lobes, the position of the brood pouch, the length of the larval trunk, and the number of larval adhesive organs.

In the Australian material examined in the course of the present study the same range in each of these characters exists as that found in the New Caledonian species combined. However, the same combinations have not been found. Specimens from the Capricorn Group, one coloured 'toffee apple' (Ridgeway 1886: QM G989) and two purple (QM G9895 GH4384), have from 4 to 7 larval adhesive organs and the length of the larval trunk in only a single colony ranges from 0.9 to 1.2mm. Dark violet colonies from South Australia (QM GH2382) have up to 20 male follicles, as do some from the Capricorn Group (QM GH3471) coloured 'dragons blood red' (Ridgeway 1886). Generally, however, the number of testis follicles appears to increase with the size and robustness of the colony. The size of the testis also affects the curve of the proximal part of the vas deferens, which in some of the Australian specimens is markedly looped, but runs a straight course when the testis follicles are expanded. Its course is also affected by contraction of the zooid and the maturation of the ovum.

The other character that F. Monniot (1988) has invoked to justify the erection of new species in this genus is the position of the brood pouch. *Cystodytes fuscus*, *C. punctatus* and *C. violatinctus* are said to brood their larvae at thoracic level, while in *C. mucosus* the brood pouch is said to be opposite the stomach. In fact the brood pouches of the first two species appear to be in the usual position at the top of the abdomen, and in the latter species (with its brood pouch level with the stomach) the embryo is at an early stage of development, and no doubt will move anteriorly before it completes it — as the embryos in the present collections have been observed to do. Monniot appears to have overlooked the fact that the anal opening is at the posterior end of the atrial cavity. A more anterior position is an artefact resulting from distortion of zooids. Further, in this genus no incipient brood pouch develops independently of the embryo as in Holozoidae. In *Cystodytes* the egg apparently is fertilised at the base of the oviduct, and increases in size and maturity as it moves up the abdomen. It protrudes more and more from the body wall as it does so, until, at the top of the oviduct it is separated from the body wall by a sharp constriction — but never by a narrow stalk.

It is possible that the material on which Monniot (F., 1988) erected these new species of *Cystodytes* was inadequate to identify intraspecific variation — only one colony of *C. punctatus* had larvae, and these are at a early stage of development; the description of *C. fuscus* is based on a single colony; and that of *C. mucosus* on only 3. It is not impossible that new, including genetic, data could in due course, establish an objective basis on which to separate certain Pacific and Australian populations of *Cystodytes* from *C. dellachiajei*. However, currently it is not possible. *Cystodytes hapu* Monniot and Monniot, 1987 has no characters justifing its separation from the present species.

Genus **Polycitorella** Michaelsen, 1924

Type species: *Polycitorella mariae* Michaelsen, 1924

Polycitorella contains species with calcareous spicules in the test, zooids with more than 4 rows of stigmata, a moderately long oesophageal neck, gonads in the posterior end of the abdomen, 6-lobed branchial and atrial apertures (each opening separately to the exterior), outer longitudinal muscle bands that extend the whole length of the zooid and an inner layer of circular muscles. The test is firm, rigid and packed with bladder cells. Zooids are usually arranged in circles to form rudimentary systems as in *Cystodytes* and *Eudistoma*.

An unusual circular constrictor muscle is around the outside of the zooid at the top of the oesophageal neck as in *Cystodytes*. This muscle is completely embedded in the test which at this level partially separates the cavity in which the zooid is contained into an upper thoracic and a lower abdominal compartment. This constrictor muscle is almost completely separate from the zooid, its attachment to it being only tenuous, and often is found completely isolated from the zooid — left behind in the test when the zooid contracts. The zooid musculature is strong and zooids are strongly contractile, often being found with the abdomen bent up against the thorax as in *Cystodytes*. On contraction, zooids withdraw from the surface as in other genera of Polycitoridae. Contracted zooids are often found in the abdominal test compartment in the lower half of the colony (as they are in *Cystodytes*).

Michaelsen (1924) reported specific organs for the formation of spicules on each side of the upper part of the oesophageal neck. These were not detected in any of the specimens examined in the course of the present study, although in many an oval mass of crowded, small spicules is embedded in the test at each side of the posterior end of the endostyle. These may be spicule-forming sites as are the lateral organs of the Didemnidae.

The genus resembles *Polycitor* in its numerous rows of stigmata, position of the gonads, separately opening 6-lobed apertures, and its larvae with median adhesive organs and lateral ampullae. It is distinguished by the constrictor muscle and the calcareous spicules in the test. The spicules resemble those of the Didemnidae although no direct phylogenetic relationship is implied.

A single embryo is brooded in a pouch that projects from the top of the oesophageal neck. Larvae are known for *Polycitorella coronaria* Monniot, 1988 (> *P. mariae*: Millar, 1963a) and *P. orientalis* n.sp. (> *P. mariae*: Monniot, 1988). They have a large trunk, ectodermal ampullae, and wide adhesive organs on relatively long stalks. The adhesive organs resemble those of *Cystodytes*, the axial protrusion constricted basally to form a wide mushroom-shaped conical protrusion resembling the axial cone of *Distaplia* rather than the flat-topped cylinder of *Polycitor* and *Eudistoma*.

The general shape and contractibility of the zooids, their arrangement in circular systems, the firm, rigid test packed with bladder cells, the circular abdominal muscle, the brooding of a single embryo at the top of the abdomen, the capacity to form calcareous spicules, and the shape of the larval adhesive organs, suggest a relationship with *Cystodytes*. *Polycitorella* is distinguished by its more numerous rows of stigmata, and the shape of the spicules which are stellate rather than flat and saucer-shaped

Previously *Polycitorella* was known only from single colonies from the Indian and western Pacific oceans — the Gulf of Suez, South Africa, the North I. (New Zealand) and Port Phillip Bay (Victoria). The 2 species described below are the only ones for which numerous specimens are now available, and these indicate a high degree of intraspecific diversity. The known species appear closely related.

The genus appears confined to the Indo-West Pacific. In addition to the 2 Australian species, the following are known, but have not been recorded from Australia:

Polycitorella hospitiolis (Savigny, 1816) > *Eucoelium hospitiolum* Savigny, from the Gulf of Suez resembles *Polycitorella orientalis* n.sp.

in the distribution of its spicules, but has fewer (6) rows of stigmata.

Polycitorella mariae Michaelsen, 1924 from the North I., New Zealand is a stalked colony with debris attached to the stalk, without circular systems, and with small (0.018 to 0.025mm diameter) spicules (ZMC 2.1.1918).

Polycitorella pallida Millar, 1962 from South Africa has a large, sessile colony, stellate spicules up to 0.06mm diameter, but zooids are not arranged in systems.

Polycitorella pérèsi Plante and Vasseur, 1966 from Madagascar has brick-red colonies and spicules up to 0.03mm with flat-ended rays.

Polycitorella setoensis Nishikawa, 1980 from Japan has unusual disc- shaped spicules as well as stellate ones.

Polycitorella coronaria Monniot, 1988

(Fig. 68. Plate 14e)

Polycitorella coronaria Monniot, 1988, p. 228.
Polycitorella mariae: Millar, 1963a, p. 711.

Distribution

New Records: Western Australia (Northwest Cape, WAM 828.83; Shark Bay, WAM 818-9.83 *QM GH2143-4*; Abrolhos, WAM 820.83 *QM GH2143*, WAM 824.83 826.83 829.83 191.88 214-6.88 220.88 222.88 233.88; Cervantes I, WAM 194.87; Cockburn Sound, WAM 842.83 *QM GH2125*, WAM 844.83 *QM GH2124*). South Australia (Great Australian Bight, Ward I, QM GH924 GH2377, NTM E33; Pearson I., QM GH1313).

Previously Recorded: South Australia (Great Australian Bight — Monniot, F. 1988). Victoria (Port Phillip — Millar 1963a).

The species is recorded from 3 to 190m. It is common off southern and western Australia as far north as Northwest Cape. It has not yet been recorded from tropical waters of the western Pacific, although, strangely, Monniot (F., 1988) described it (from a single colony from the Great Australian Bight) in a paper on ascidians from New Caledonia.

The numerous specimens examined in the present study has made it possible to more fully document the species; and to emphasise one of its main characteristics — the regular cushion-shape of the larger specimens — which, despite the species name, was not altogether apparent from the single crescentic colony on which the original description was based. Sadly, despite the large number of specimens already available in Australian museums, the holotype of this common Australian species is lodged in the Muséum National d'Histoire Naturelle, Paris, having been donated by the US National Museum (see Monniot, F., 1988).

Description

External Appearance: Most of the recorded colonies are massive circular, oval or long and slightly convex cushions up to 6cm in maximum dimension and about 3cm high. Large colonies are fixed by the whole of the basal surface. When it is curved over rubble or other substrates the whole colony becomes dome-shaped. Smaller colonies usually have a thick stalk, up to 3cm long, with a slightly wider almost spherical to dome-shaped head. The stalk is progressively lost as the colony increases in size, the head increasing in diameter and becoming flatter on the upper surface.

Colonies show considerable colour variation, which is affected by the distribution of dark spherical pigment cells and white calcareous spicules. The upper surface is white, grey or black with black or white patches where the apertures open to the surface. The lower half of the colony is always a dirty white colour. Pigment cells are present in the test of the upper surface, and sometimes in the thin layer that curves in to line each siphon. They are present also around the zooid compartments in the test. Pigment cells are also scattered sparsely in the internal test of the upper part of the colony, becoming more sparse toward the base. White calcareous spicules are always in the external test of the stalk and usually (but not always) in the basal half of the colony. They are also in the internal test of the lower half of the colony around the abdominal parts of the zooids. Spicules are usually mixed with pigment cells in the surface layer of test over the upper part of the colony making it grey. The upper part of the colony is black if spicules are absent from the surface test. Spicules are in the surface test only around the apertures creating a pattern of white patches where the zooids open to the surface. Internally spicules are always absent from a thin layer of test that lines the cavities containing the zooids. Otherwise they are either throughout the internal test, only in patches or in a layer at the upper abdominal level, or only in the upper half of the colony, or absent altogether from the top half. Spicules are stellate, 0.04 to 0.08mm diameter, with 5 to 7 conical rays in optical section. Sometimes mulberry-like spicules with rounded rays also occur. Oval masses of small, crowded spicules are sometimes visible at each side of the posterior end of the endostyle, embedded in the otherwise spicule-free layer of test that lines the cavities containing the zooids. Although no actual sac connected to the body wall of the zooid was detected, these oval masses of small spicules probably are where spicules are generated.

Zooids are always in evenly spaced circular systems of 7 to 10 zooids, the 6-lobed branchial apertures present in a wide outer circle with the 6-lobed atrial apertures, on the end of relatively long siphons opening in a small tight inner circle

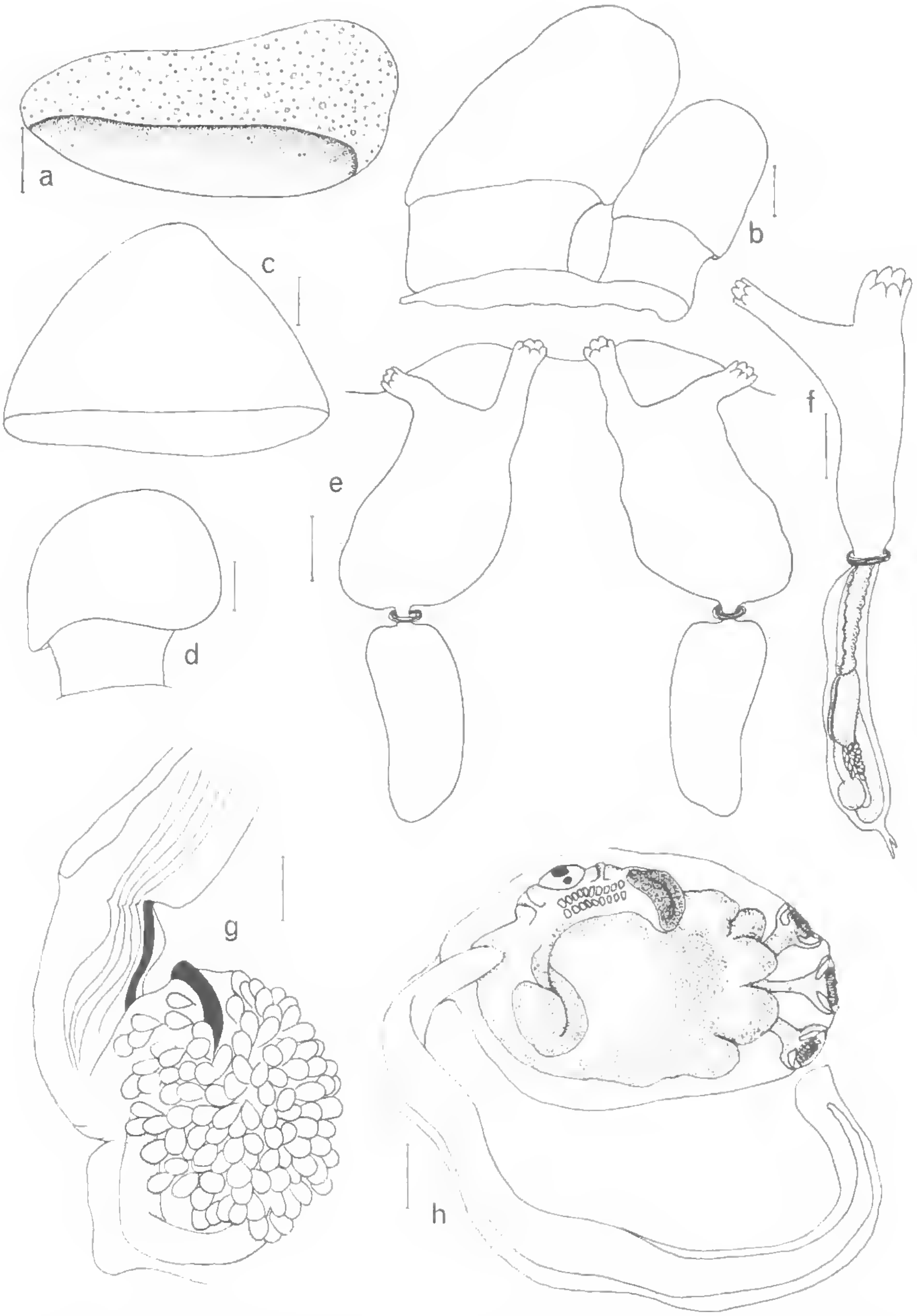


FIG. 68, *Polycitorella coronaria*: **a**, large colony showing arrangement of zooid openings in circles (WAM 844.83); **b–d**, outline of various colonies (WAM 818.83 826.83 824.83); **e**, a section through a system showing zooids embedded in the test with atrial openings near centre of circle, and branchial openings in the outer circle (WAM 216.88); **f**, zooid showing long atrial siphon and oesophageal constrictor muscle (WAM 214.88); **g**, posterior end of thorax and contracted abdomen showing detail of testis and vas deferens (WAM 819.83); **h**, larva (QM GH1313). Scales: **a**, 2cm; **b–d**, 1cm; **e**,**f**, 1mm; **g**, 0.5mm; **h**, 0.2mm.

sometimes around a central depression. The centres of the systems are about 5mm away from one another. The atrial apertures are on long siphons that reach into the centre of the circle and, when open and extended, the anterior atrial lobes are longer than the posterior ones — a phenomenon commonly observed where atrial siphons open in the centre of incipient circular systems (see *Eudistoma*)

The test is firm and, when spicules are absent, it is glassy, transparent and packed with bladder cells. Zooids are accommodated in large, rigid hourglass-shaped compartments in the firm test, the thoracic and abdominal section of each compartment separated by the test constriction with its embedded constrictor muscle.

From the condition of the zooids, apparently the whole zooid withdraws from the surface on contraction. The constrictor muscle sometimes has contracted around the top of the abdomen before the thorax is withdrawn into the abdominal chamber, and it is assumed that this usually would occur in life. In some of the material examined however, contraction has been so violent that the zooid has lost its attachment to the muscle, and has completely withdrawn into the abdominal compartment. In other specimens the contracted constrictor muscle has strangled the thorax at various points along its length as it was being withdrawn into the abdominal compartment — sometimes contracting around the top of the thorax and strangling the zooid behind the siphons or occasionally catching only the two siphons.

INTERNAL STRUCTURE. Test compartments containing the zooids are about one to 2cm in total length. It is assumed that living zooids completely fill these spaces. The thorax and abdomen appear of almost equal length in their extended condition. Contracted zooids are from 4 to 8mm. The branchial aperture is terminal, and the atrial aperture extends obliquely on the end of its long siphon into the centre of the circular system of zooids. Externally there are about 20 longitudinal muscles on each side of the thorax and these continue in wide bands along each side of the abdomen. A layer of inner circular muscles is present beneath the longitudinal ones on the thorax. Sphincters surround each aperture, and the constrictor muscle (described above) is at the top of the abdomen.

Twelve long branchial tentacles alternate with shorter ones in a single circle at the base of the branchial siphon, although difficult to count. There are 10 to 20 rows of 15 to 30 stigmata. The number of stigmata appear to increase with the size of the colony. Dorsal languets are triangular and present in the mid-line.

The oesophagus is vertical in partially relaxed zooids (WAM 214.88) and opens into the long stomach in the posterior half to one-third of the abdomen. The stomach wall is smooth externally, and has papillations internally. It is not folded. There is a short duodenal area and a small rounded posterior stomach constricted from the rectum in the pole of the gut loop.

When mature, the testis is large, consisting of a mass of numerous short follicles that project out from the loop of the gut. The vas deferens arises from the center of the mass and loops out around the outside of the anterior half of the mass before it extends anteriorly up the oesophageal neck to the atrial cavity. Only a single egg at a time was found outside the male follicles.

South Australian specimens had mature gonads and larvae in March (QM GH1313) and April. In the Western Australia material they were also mature in some (but not all) specimens from Cervantes and from the Abrolhos collected in March and April. A large embryo is in the oviduct at the top of the abdomen in one colony only (QM GH2377). Larvae also are present in the brood pouch at the top of the oesophageal neck in the specimen from Port Phillip (Millar 1963: BM85.11.20.48). The larval trunk is 1.1 to 1.2mm long and has 4 pairs of lateral ampullae alternating with the 3 median adhesive organs at the anterior end.

REMARKS: This species is variable in colour pattern (though not in colour) and in the shape of the colony. The colour is always some combination of black and white — the former varying according to the distribution of the black pigment cells, and the latter according to the distribution of the calcareous spicules. Variations in the shape of the colony depend on its size and the nature of the substrate.

Polycitorella coronaria is readily distinguished from previously described species by the arrangement of its zooids in circular systems emphasised by the colour patterns in the colonies. Further, the spicules of the present species are larger than those of the New Zealand species *P. mariae*, which have a maximum diameter of 0.025mm. Spicules of *P. pallida* from South Africa are larger (to 0.06mm diameter) and are similar to those of the present species. Millar (1963a) observed the test constriction between the abdominal and thoracic compartments, but overlooked the muscle embedded in it. *Polycitorella mariae*: Millar, 1963a from Port Phillip (Victoria) has spicules of 0.06mm diameter, and although Millar observed only mulberry-like spicules with rounded rays, the specimen probably belongs to the present species. Similar spicules do occur in specimens from Western Australia, although they are mixed with stellate ones. Larvae of the Victorian specimen are identical with those from South Australia.

Polycitorella orientalis has smaller colonies, its largest spicules are less than half the size of those in the present species, zooids are only occasionally grouped into small systems, and the larval trunk is almost twice the size of that of the present species (see F. Monniot 1988).

Polycitorella orientalis n.sp.

(Fig. 69. Plate 14f,g)

Polycitorella mariae: Monniot. F., 1988, p. 227.

Distribution

Type Locality. Queensland (Swain Reefs, under ledge 8m, AMPI 133, coll. N. Coleman, 9.7.74, holotype QM G9477, paratype QM GH4420; coll. J. Watson 10.10.74, paratype QM GH4420).

Further Record. Queensland (Heron I, specimen destroyed for analysis: Fredrickson 1978; Coral Sea — Monniot. F. 1988).

Description

External Appearance. The specimens have relatively small (about 1cm diameter) rounded heads on a short stalk of slightly less diameter. The whole colony is 1 to 2.5cm high. A larger colony (QM GH4420) of 2cm diameter is a flat cushion without a stalk. Zooids open onto the upper surface of the head on well separated shallow, oval prominences. Some are grouped into 2- or 3-zooid systems, their atrial apertures adjacent to one another. The zooids converge into the centre of the head and down into the stalk, almost to the base.

In life colonies are cream, pale yellow or green, but when preserved. they always are cream.

Calcareous spicules are in the surface layer of test of the head and the stalk. Internally, they are only sparse at thoracic level and in the stalk they form a sheath around each abdomen. They are absent from the test between these abdominal sheaths. Spicules are 0.025 to 0.035mm in diameter. They vary from stellate, with 5 to 15 pointed or flat-ended rays in optical section, to mulberry-like spicules with rounded rays, and spherical ones made of many thin radially arranged rods.

Internal Structure. Contracted zooids are about 5mm long. The apertures are 6-lobed, both on short siphons at the anterior end of the body. In addition to sphincters around the apertures, the thoracic musculature consists of longitudinal bands overlying a layer of circular muscles.

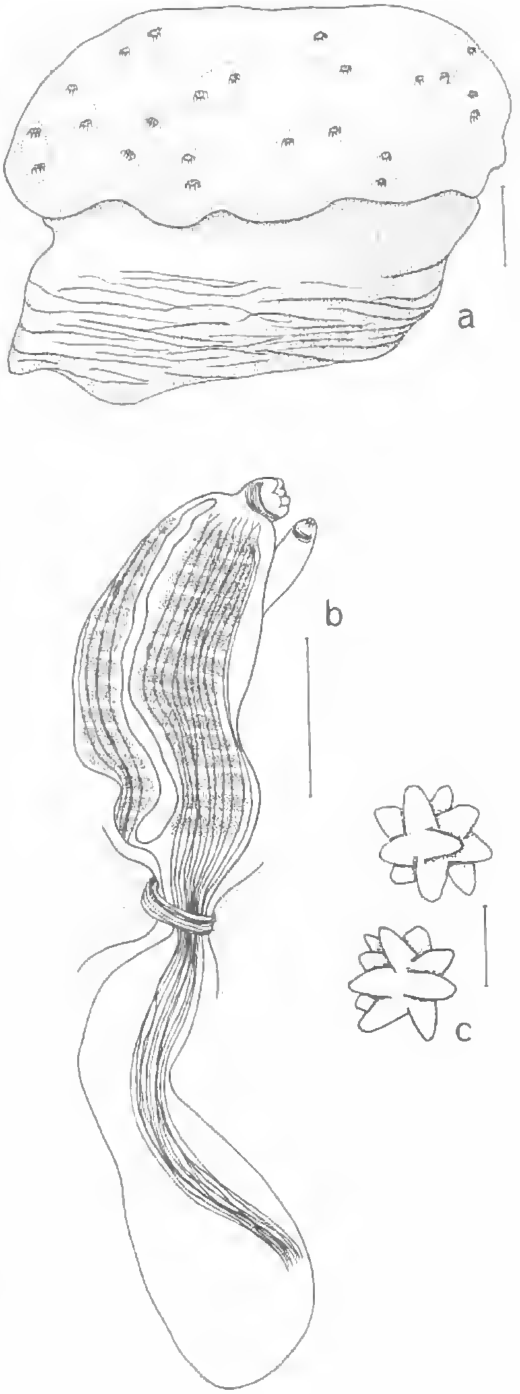


Fig. 69. *Polycitorella orientalis* n.sp. (holotype QM G9477): **a**, colony; **b**, zooid showing circular muscle embedded in the test around top of oesophagus; **c**, stellate spicules. Scales: a, 2mm, b, 1mm; c, 0.02mm.

Longitudinal bands extend along the abdomen in a pair of ventral muscles. The constrictor muscle is embedded in the test around the upper part of the oesophageal neck. There are 10 rows of about 20 long stigmata.

The thorax and abdomen may be of equal length in relaxed zooids. However, in these variously contracted specimens the abdomen is sometimes shorter and sometimes longer than the thorax. The stomach is in the posterior third of the abdomen. It has fine longitudinal glandular ridges in the internal lining, but it is not folded. A mass of crowded, short, pyriform, male follicles is in the gut loop. No eggs were seen in the newly recorded material.

Larvae of this species were in specimens from the Coral Sea (Monniot, F. 1988). The larval trunk is 1.9mm long, and the tail barely reaches to its anterior end. There are 4 pairs of lateral ampullae alternating with the 3 adhesive organs in the anterior mid-line, an ocellus and otolith.

REMARKS: *Polycitorella orientalis* is distinguished from *P. coronaria* by its small colonies, its colour (lacking the dark pigment of the latter species), its small systems that occur only occasionally, its relatively small spicules with slightly longer arms and its appreciably longer larval trunk. Although the now destroyed specimen from Heron I. had a preponderance of mulberry-like spicules like the specimen of *P. coronaria* from Port Phillip Bay (> *P. mariae*: Millar 1963a), the spicules in the Heron I. colony were the same size as those of the present species, and the colony form and pigmentation were also similar.

Monniot (F. 1988) believed *P. mariae*: Millar 1963a (from Port Phillip Bay — not the Philippines) was a synonym of her specimen from Chesterfield Is in the Coral Sea. However, the spicules of the Victorian specimens are larger and the larval trunk is shorter (1.2mm) than that of the Chesterfield Is specimen (1.9mm). The Chesterfield Is specimen appears conspecific with the present species, having similar yellow colonies, and small spicules. F. Monniot (1988) also thought that the Chesterfield Is specimen was a synonym of the New Zealand *P. mariae* Michaelsen (ZMC 2.1.1918). However, although the New Zealand species has a similarly stalked colony, its stalk is longer and covered with adherent foreign particles, its spicules are smaller than those of the present species and they are all stellate with conical rays.

Polycitorella pallida from South Africa like *P. coronaria* forms larger colonies and has larger spicules.

Genus **Eudistoma** Caullery, 1909

Type species: *Distoma rubrum* Savigny, 1816.

The genus has small, characteristically polycitorid zooids with a long oesophageal neck, and gonads and stomach at the posterior end of the abdomen. The atrial and branchial apertures are 6-lobed. Longitudinal muscle bands on the thorax extend in one or 2 bands along each side of the abdomen. An inner layer of circular muscle lies beneath the longitudinal ones on the thorax. There are 3 rows of stigmata. The anterior row contains more stigmata than the other two, and its dorsal end usually curves anteriorly along each side of the mid-dorsal line. The stomach is always small, shield-shaped and smooth. A long duodenal area is posterior to the stomach, and usually an oval posterior stomach at the distal end of the descending limb of the gut loop. The gastro-intestinal gland is well developed. The anus opens between the second and third rows of stigmata. As in other genera of the Polycitoridae, zooids withdraw into the base of the colony when disturbed.

With rare exceptions (when it occurs in the distal part of the oviduct), fertilisation takes place in the atrial cavity. Larvae are small, with a larval trunk only occasionally more than 1mm long. They have 3 stalked adhesive organs in the vertical mid-line anteriorly. A fairly wide tuft of columnar cells project from the centre of a deep ectodermal cup. Ectodermal ampullae usually alternate with the adhesive organs and often also are along each side of the anterior end of the trunk. Ectodermal vesicles, originating as terminal expansions of thread like extensions from ectodermal cells, are often present in the larval test (see Annotated Glossary: **larvae**).

Sand and other foreign particles including plant cells are often embedded in the test, sometimes confined to the central or basal part of the colony, but sometimes throughout the test. In most species faecal pellets are in the test. This may result from the contraction and withdrawal of zooids from the surface causing ejection of faeces from the short thorax. Several species also have unusually large spherical cells embedded in the test. Michaelsen (1930) believed these symbionts, although this is established only for *E. amplum*. The test is often brightly pigmented and usually opaque in living specimens.

Zooids of most species are in rudimentary circular systems with the atrial apertures in the centre of the circle. In these species the atrial siphons are long. When systems are absent the atrial siphons are shorter and more or less the

TABLE 8. SUMMARY OF CHARACTERS OF SPECIES OF *EUDISTOMA* RECORDED FROM AUSTRALIA

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Colonial systems	Test colour	Sand in test	[3]Pigment or vesicular cells in test (max. diameter mm)	[4]Larvae (no. incubating) trunk length (mm)	Other
E. laysani	WP,tr	Botany Bay –Sarina	numerous stalked conical or rope-like lobes	none	whitish –blue	none	—	(8) 0.4–0.5	—
E. elongatum	A,st	Jervis Bay –Hervey Bay	″	″	″	″	—	(8) 0.5	no lateral larval ampullae
E. superlatum n.sp.	A,tr	Dampier Arch.–Abrolhos	″	″	pink?	″	—	—	colony massive: zooids with a long vascular stolon
E. globosum	A,tr	Abrolhos–Margaret River; Heron Is	almost sessile spherical heads	″	blackish green	absent only from outer test on head	pigment cells (0.04) beneath surface	(1) 1.7	—
E. glaucum	WP,tr	Heron I. –Lizard I.	″	zooids in circles	opaque green	in stalk only sparse	minute pigment cells throughout	(2) 1.2	moderately long vascular stolon; preservative stains green
E. tumidum n.sp.	I,tr	Gulf of Carpentaria	″	?	?	none	?	(4) 0.5	pointed lateral larval ampullae with parietal branches
E. malum n.sp.	A,tr	Capricorn Gp	″	″	yellow, brown, purple	″	minute pigment cells (0.01) throughout	(4) 0.75	sand on stalk
E. gilboviride	WP,tr	Heron I. –Lizard I.	wedge-shaped lobes	″	green with yellow	″	minute pigment cells (0.02) crowded in surface	(2) 0.9	leaf-shaped larval ampullae
E. aureum n.sp.	A,te	South Australia	single stalked lobe	″	yellow	″	?	?	—

continues over page . . . . .

TABLE 8. SUMMARY OF CHARACTERS OF SPECIES OF *EUDISTOMA* RECORDED FROM AUSTRALIA (CONTINUED)

Species	[1]Biogeographic description	[2]Range around Australia	Colony shape	Colonial systems	Test colour	Sand in test	[3]Pigment or vesicular cells in test (max. diameter mm)	[4]Larvae (no. incubating) trunk length (mm)	Other
E. purpureum n.sp.	A,tr	Capricorn Gp	sessile cushion	"	opaque purple	in basal test only, sparse	"	(2) 1.5	bract-like median larval ampullae
E. eboreum n.sp.	A,tr	Lizard I.	"	"	whitish	"	brown-orange pigment cells (0.01) throughout	(1) embryo only 1.0	fusiform and branched dendritic cells throughout
E. muscosum nom. nov.	WP	Heron I.–Lizard Is.	"	"	olive–brown	"	tan pigment cells (0.04) crowded at mid-level, pigment cells (0.03)	(2) 1.0	larval trunk spherical; preservative stains red-brown
E. pratulum n.sp.	A,tr	Heron I.	"	"	cream–sage green	none	brown pigment cells (0.03) throughout	(1) embryo only 0.75	test firm; surface rough; zooids green
E. anaematum n.sp.	A,tr	Capricorn Gp	"	"	pink, brown, olive	basal half of colony only	minute pigment cells (0.01) sparse	embryo only 0.8 in oviduct	—
E. incubitum n.sp.	A,tr	Capricorn Gp	small stalked mushroom-like	"	white	none	vesicles (0.05) evenly spaced in surface	(4) 0.6 in oviduct	vesicles at surface of larval test
E. maculosum n.sp.	A,te	Pt. Peron-Jervis Bay	thick sheet	"	2 toned	at mid-level only	brown, tan pigment cells in patches in surface	(1) 0.9	bract like larval ampullae
E. tigrum n.sp.	WP,tr	Heron I.–Abrolhos	"	"	"	sparse basally	dark pigment cells in surface surround translucent patches	(3) 0.75	median larval ampullae only
E. amplum	WP,tr	Heron I.–Lizard I.	"	"	colourless	variable	red and green symbionts (0.3)	(2) 1.0	—

E. gracilum n.sp.	A,tr	Heron I.	thin sheet	?	red	none	minute pigments cells throughout	(1) 0.6	test very soft; zooids minute
E. constrictum n.sp.	A,te	South Australia	rounded cushions	none	colourless	sand throughout	—	(4) 1.0	constricted around oesophagus
E. microlarvum n.sp.	A,st	Moreton Bay –Hervey Bay	thick sheets upper surface lobed	"	colourless	crowded at mid-level	—	(1) 0.4	zooids minute thread-like
E. sabulosum n.sp.	A,te	Gt Australian Bight–Western Port	"	zooids in circles	"	sand throughout	—	(6) 0.5	lateral ampullae only
E. ovatum	WP,tr	Hervey Bay –Cape Boileau	thick sheets	"	"	"	—	(5) 0.6	branched lateral ampullae
E. pyriforme	WP,tr	Bundaberg –Torres St	wedge-shaped to rounded lobes	zooids in single circle/lobe	"	"	—	—	common basal test
E. bulbatum n.sp.	A,te	New South Wales	cylindrical lobes	"	?	"	—	—	base of colony produced into roots
E. angolanum	IWP,tr	Lizard I.–Cape Boileau	irregular cushions or sheets	cloacal cavity present	red	crowded throughout	—	(3) 1.0	larvae with 3 rows of lateral ampulla
E. carnosum n.sp.	I,tr	Abrolhos–Rottnest I.	thick sheets	"	?	absent from surface of systems	red symbionts? (0.5)	(1) 1.5	"
E. reginum n.sp.	A,tr	Capricorn Gp	thick sheets	"	red	"	red symbionts? (0.3)	(3) 1.0	colony hard

[1] WP, West Pacific; I, Indian Ocean; IWP, Indo-West Pacific; A, indigenous; tr, tropical; te, temperate. [2] Range given anti-clockwise around the continent. [3] Description of cells observed in preserved colonies only. [4] Incubation in atrial cavity unless oviduct indicated.

same length as the branchial siphons. Both siphons usually have a distinct sphincter muscle.

Eudistoma is distinguished from *Sigillina* — which also has only 3 rows of stigmata — by the long oesophageal neck, much smaller zooids, absence of a brood pouch, smaller embryos incubating in the atrial cavity, and absence of the epicardial extension in the vascular stolon. The structure of the gut with its long duodenal region, oval posterior stomach and small, smooth stomach, is particularly stable throughout *Eudistoma* and constitutes a further reliable distinguishing character. Although the larval adhesive organs have a more or less flat-topped central protrusion of columnar cells, it is always cylindrical and never forms a long ridge or platform as it does in *Sigillina*.

The genus is an homogenous one, and zooids are difficult to distinguish from one another. They are invariably found contracted, causing various distortions of the gut and abdomen. Hastings (1931) observed that kinks in the gut, used by many authors to distinguish species, are of little value as taxonomic characters. While the oesophagus becomes wrinkled on contraction, the rectum, containing faecal pellets, is variously kinked and sometimes looped in contracted zooids of all species. Characteristics of the colony — its shape, colour and test inclusions — afford more reliable characters for species identification than the zooids themselves. Unfortunately the colour is lost in preserved material and test inclusions have not always been recorded. The difficulties encountered in characterising *Eudistoma* spp. cannot be over-emphasised, but to some extent at least, these will be alleviated if records are kept of the colour and general appearance of living colonies.

In a few cases species share conspicuous characters that suggest a phylogenetic relationship. Thus *Eudistoma angolanum*, *E. carnosum* n.sp., *E. reginum* n.sp., with *E. magalhaensis* from the Magellanic region, form a species group characterised by the localisation of pigment in pockets in the larval trunk haemocoele, and the formation of distinct, albeit rudimentary, cloacal cavities. Also *E. globosum*, *E. laysani* and *E. elongata* are possibly related, colonies all having stalked lobes, and zooids being crowded and not in systems. Other species groups have not been identified.

Eudistoma has not been recorded from the Antarctic, only one species — *E. vitreum* (Sars, 1851) — is known from boreal waters (see Millar, 1966b), and the genus is most diverse in tropical waters. Species of this genus are commonly encountered around the Australian continent. The 27 species discussed below include 17 new to science of which 11 are tropical. Six indigenous species are known only from temperate waters. Although a number of the Australian species resemble some recorded from Africa, they appear distinct. Sluiter (1909, 1919) recorded 12 species from the Indo-Pacific that can be assigned to this genus with confidence. However, in the following 80 years only 2 of these were recorded again, although a further 5 species were described from the area. Difficulties in distinguishing species from one another when only preserved material is available may have caused this apparent lack of diversity in the previously recorded material.

KEY TO THE SPECIES OF *EUDISTOMA* RECORDED FROM AUSTRALIA

1. Systems present 2
   Systems not present...................23
2. Rudimentary cloacal cavity present 3
   Rudimentary cloacal cavity not present ...5
3. Sand absent from surface test around systems 4
   Sand present throughout ....*E. angolanum*
4. Cloacal apertures on conical prominences.. ....*E. carnosum* n.sp.
   Cloacal apertures not on conical prominences ....*E. reginum* n.sp.
5. Colonies divided into numerous lobes on common base 6
   Colonies not divided into numerous lobes on common base 8
6. Sand crowded throughout test........... ....*E. pyriforme*
   Sand not crowded throughout test 7
7. Colony lobes top-shaped .....*E. gilboviride*
   Colony lobes rounded, sessile ....*E. tumidum* n.sp.
8. Large (up to 0.3mm) symbiotic plant cells present in test ....*E. amplum*
   Large symbiotic plant cells not present in test 9
9. Sand crowded throughout test..........10
   Sand not crowded throughout test 12
10. Colonies upright cylinders ....*E. bulbatum* n.sp.
    Colonies not upright cylinders..........11
11. Sand present around apertures of zooids; tropical species ....*E. ovatum*
    Sand not present around apertures of zooids; temperate species.....*E. sabulosum* n.sp.
12. Colony with two-toned pattern in surface test 13
    Colony without two-toned pattern in surface test 14

13. Larval trunk 0.9mm long; temperate species .... *E. maculosum* n.sp.
Larval trunk 0.6mm long; tropical species .... *E. tigrum* n.sp.
14. Fusiform and dentritic pigment cells present .... *E. eboreum* n.sp.
Fusiform and dentritic pigment cells not present 15
15. Surface test speckled with evenly spaced vesicles (0.05mm diameter) .... *E. incubitum* n.sp.
Surface test not speckled with evenly spaced vesicles 16
16. Colonies extensive investing sheets 17
Colonies not extensive investing sheets ..18
17. Test soft and mucus-like .. *E. gracilum* n.sp.
Test not soft and mucus-like .... *E. pratulum* n.sp.
18. Test bright green both living and in preservative .... *E. glaucum*
Test not bright green either living or in preservative 19
19. Test bright purple in life; zooids greenish-black in preservative .... *E. purpureum* n.sp.
Test not bright purple in life; zooids not greenish black in preservative 20
20. Colonies with sand embedded in stalk ...21
Colonies without sand embedded in stalk 22
21. Layer of sand beneath surface test; zooids reddish-brown in preservative .... *E. aureum* n.sp.
No layer of sand beneath surface test; zooids not reddish-brown in preservative .... *E. malum* n.sp.
22. Surface test with conspicuous white suspension in preservative; zooids not reddish-brown in preservative .... *E. anaematum* n.sp.
Surface test without conspicuous white suspension in preservative; zooids reddish-brown in preservative .... *E. muscosum* nom. nov.
23. Colonies stalked 24
Colonies not stalked 26
24. Sand present both in stalk and in centre of head .... *E. globosum*
Sand not present either in stalk or in centre of head 25
25. Head long and cylindrical .... *E. elongatum*
Head not long and cylindrical ... *E. laysani*
26. Colony with embedded sand 27
Colony without embedded sand .... *E. superlatum* n.sp.
27. Sand absent from surface test over anterior ends of zooids ...... *E. constrictum* n.sp.
Sand not absent from surface test over anterior ends of zooids .... *E. microlarvum* n.sp.

The following species, previously described from the western Pacific and the Indonesian region, have not yet been recorded from Australia:

Eudistoma fragum F. Monniot, 1988 from New Caledonia has a red test, embedded sand, and a larva with lateral ampullae similar to those of *E. amplum*. However, symbiotic cells have not been recorded, and the zooids are not arranged in circles.

Eudistoma glabrum (Sluiter, 1919) has sessile, cushion-like colonies with a convex upper surface about 2cm high in the centre. Little sand is embedded in the upper layer of test and elsewhere the test contains only crowded faecal pellets. Zooids are in circular systems. Branchial and atrial siphons are both long, and the basal part of the branchial siphon has a wide band of numerous branchial tentacles in at least 7 rows. About 25 stigmata are in the anterior row, which extends forward along each side of the mid-dorsal line. Spherical pigments cells of about 0.01mm diameter are scattered evenly, but sparsely, throughout the test. It is distinguished from *E. malum* by its long branchial siphon and wide band of branchial tentacles (ZMA TU1281 lectotype).

Eudistoma laysani: Tokioka, 1967a, from the Palau Is has a similar, although less regular colony than *E. toealensis* Millar, and is further distinguished by its median rather than paired larval ectodermal ampullae that alternate with the median adhesive organs.

Eudistoma loricatum (Sluiter, 1909) from Indonesia has a colony similar to *E. bulbatum* n.sp. However in *E. loricatum* the lobes of the colony are smaller, devoid of sand over the upper surface and are attached to common basal test (ZMA TU1267 lectotype).

Eudistoma miniacum (Sluiter, 1909) from Indonesia has flat-topped lobes of variable diameter arising from a common base, larvae with a long cigar-shaped trunk (1.2mm long) and 4 median ectodermal ampullae alternating with the adhesive organs and zooids in conspicuous circular systems opening on the upper surface of the lobe. The lobes have a distinctive appearance, with a network of pink pigment cells in the surface test (ZMA TU1268 lectotype).

Eudistoma multiperforatum (Sluiter, 1909) forms hard, sand-impregnated, bluish-red sheets with a superficial resemblance to colonies of *E.*

angolanum. The sand is crowded in the lower half of the colony and sparse elsewhere. Zooids are large and pink in preservative, not crowded, not arranged in circular systems, and lack long atrial siphons (ZMA TU809.1–.2 syntypes). *Eudistoma* sp. aff. *angolanum*: Tokioka 1967a from the Palau Is may be conspecific.

Eudistoma rubrum Tokioka, 1954a from the Tokara Is and Fiji (Kott 1981) has almost spherical, transparent heads with reddish-orange zooids. The spherical transparent heads are unusual — resembling *Polycitor* more closely than *Eudistoma* spp.

Eudistoma segmentatum (Sluiter, 1909) from Indonesia forms upright, cylindrical or conical lobes arising from a common basal test mass. The tops of some of the lobes of the lectotype appear regenerating, thus accounting for variations in the shape of the zooid-bearing part. Zooids in these regenerating colonies are apparently non-functional juveniles, as they do not open to the exterior and no faecal material is present in the gut. The species is distinguished from *E. loricatum* and *E. laysani* by its more numerous zooids and taller colonies. Constrictions in the test recorded for this species were not distinguishable on examination of the lectotype (ZMA TU1268 lectotype).

Eudistoma stellatum Monniot, 1988 from New Caledonia apparently resembles *E. angolanum* in the field. However, the latter species has a larva with more numerous ampullae. The fold in the stomach described for this species does not appear to have a homologue in the genus. The larva is like that of *E. gilboviride*.

Eudistoma toealensis Millar, 1975 from Indonesia has rather long cylindrical lobes arising from a common basal test mass, and a long larval trunk of 1.0 to 1.3mm. These colonies resemble some from Vietnam assigned to *E. laysani* by Tokioka (1967b) which have the same partially subdivided, paired larval ectodermal ampullae and the same posterior extension of the ventral ampulla as Millar's specimens.

Eudistoma tokarae Tokioka, 1954a from the Tokara Is has zooids opening on the upper surface of small upright lobes, and faecal pellets and abdomina in the stalk. Minute dark greenish pigment spots are in the test, and zooids. Tokioka and Nishikawa (1975) discussed the possibility that this species represents juvenile colonies of *E. glaucum*. However, both the zooids and colonies, including the pigmentation, are different from those of *E. glaucum*. Although the colonies are more like *E. laysani* and *E. incubitum* n.sp. the pigmentation is different from both, and *E. tokarae* appears a good species, distinguished from others by its dark pigment cells in the test and zooids.

The following species with 3 rows of stigmata, which were assigned to *Polycitor* by Sluiter (1909), are not members of *Eudistoma*: *P. violaceus* (ZMA TU814 holotype < *Trididemnum* sp.), *P. signiferus* (ZMA TU808.1 lectotype < *Sigillina signifera*), *P. coalitus* (< *Hypodistoma deerratum*), and *P. ianthinus* (< *Exostoma* n.gen. *ianthinum*). The last three species are discussed in this work.

Eudistoma amplum (Sluiter, 1909)

(Fig. 70, Plate 15a)

Polycitor amplus Sluiter, 1909, p. 21. **Not** Hartmeyer, 1919, p. 105 (see Hastings, 1931).

Eudistoma amplus: Tokioka, 1950, p. 118.

Eudistoma amplum: Tokioka, 1967a, p. 121. Millar, 1975, p. 219 (part, not specimen from Toeal with cloacal cavity < ? *E. reginum* n.sp.).

Polycitor discolor Sluiter, 1909, p. 17.

DISTRIBUTION

NEW RECORDS: Queensland (Capricorn Group, QM GH1936-7 GH1977-8 GH374 GH1824 GH1352 GH1824 GH1833-4 GH2238 GH3817 GH4421-4 GH4432 GH4442 GH4470-1 GH4477-9 GH4500-4 GH4512-7 GH4562; Green I., QM G12501; Lizard I., QM GH4608-9).

PREVIOUSLY RECORDED: Palau Is. (Tokioka 1950, 1967a). Indonesia (ZMA TU781 type *Polycitor amplus* Sluiter, 1909; ZMA TU785.1–.3 syntypes *Polycitor discolor* Sluiter, 1909). Philippines (Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: The colony forms robust flat-topped cushions to sheets up to 14cm or more in maximum dimension and about 1.5cm thick, with rounded borders. The surface is smooth and often shiny. Although sand grains are present, and sometimes crowded in the test, they are usually absent from the upper surface except between the atrial and branchial openings of each zooid so that the sand forms a star-shaped or daisy-like pattern that emphasises the arrangement of zooids in circular systems. Sand grains in the surface, especially around the zooids, are smaller than those in the remainder of the test. Systems are about 0.5cm in diameter with the atrial apertures toward the centre of each circle and the branchial apertures around the periphery. The surface test is often (but not always) depressed in the centre of the circle and the atrial openings are around the border of this depression.

The test itself is glassy and colourless, but this is obscured by the test inclusions. Large, variously sized (up to 0.3mm in diameter) spherical vesicles in the test are usually (but not always) crowded in the surface layer and become less crowded

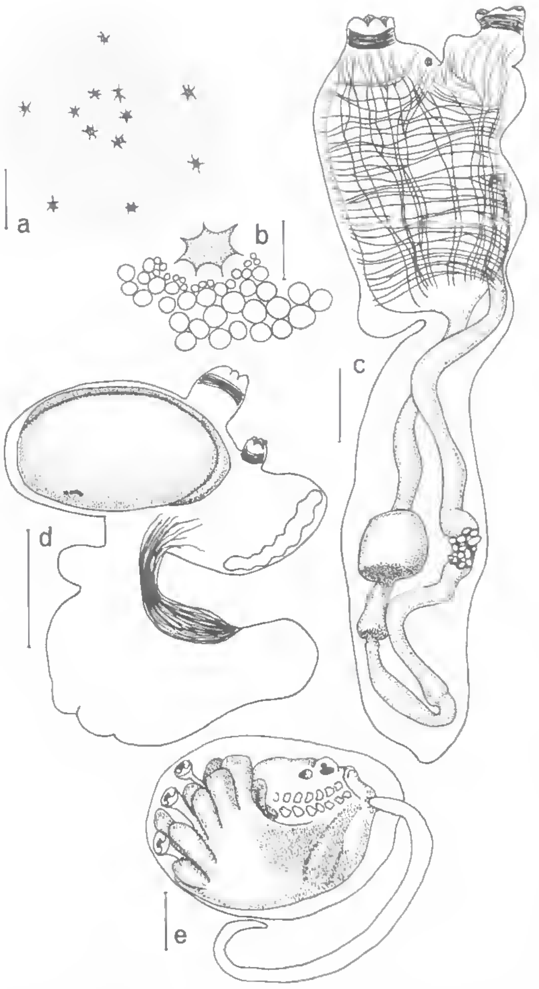


FIG. 70, *Eudistoma amplum*: **a**, branchial (outer circle) and atrial (inner circle) openings of a single rudimentary system on surface of colony (QM GH2238); **b**, embedded green cells clustering around a branchial aperture (QM G11978); **c**, zooid showing thoracic muscles and vesicles associated with the gastro-intestinal gland clustered around the gut (QM GH352); **d**, contracted zooid with larva in atrial cavity (QM G11937); **e**, larva (QM G11937). Scales: **a**, 1mm; **b**, 0.25mm; **c**,**d**, 0.5mm; **e**, 0.2mm.

toward the base. Embedded sand grains become more crowded toward the base. The spherical vesicles are eukaryotic algal cells. They are usually red and shiny in the living specimens, causing the maroon to 'aster purple' (Ridgeway 1886) and brown of the colony. This sometimes shades to brownish-yellow ('gallstone yellow': Ridgeway 1886) when sand is near the surface. However, green and red plant cells and sand are often distributed fairly evenly through the whole thickness of the colony. In preservative vesicles are cream or slightly cloudy-greenish and translucent. In one specimen (QM GH4555) the green cells are cysts containing numerous small spheres (see *E. vitiatum* Kott, 1981).

This species very often has *Prochloron* cells on the surface of the colony (Kott *et al.* 1984). They are only loosely attached and can be easily wiped off.

INTERNAL STRUCTURE: Living zooids are yellow-orange. They are robust, but when contracted are only about 5mm long. The atrial siphon is up to 3 times the length of the branchial siphon. The circular sphincters around each aperture are not especially strong. Up to 20 longitudinal muscle bands on each side of the thorax often join one another to form half that number of bands. They are relatively fine, well separated from one another, and sometimes are in 3 or 4 groups on the sides of the thorax. The circular muscles are more numerous. About 22 stigmata in each row are generally long, becoming shorter ventrally. Dorsal languets are to the left of the mid-dorsal line. About 24 branchial tentacles of various sizes are apparently in 3 circles, although this is difficult to see.

The small, smooth stomach is near the posterior end of the abdomen. There is a relatively long, narrow duodenal area and a long mid-intestine that curves around in the pole of the gut loop before entering the rectum. The posterior stomach (in the mid-intestine) is sometimes rather obscure. A band of thin-walled spherical, elongate or irregular terminal vesicles of the gastric gland surround a section of the gut opposite the stomach. A kink occurs in the proximal part of the rectum just posterior to the stomach in these contracted specimens.

Gonads are maturing in specimens collected in September but not in January, February or July. Colonies collected in July are in an active vegetative phase. One or 2 large larvae are in the atrial cavity of specimens collected from the Capricorn Group in July to September (QM G11936 7 G11971). The larval trunk is almost 1mm long, and the tail winds a little more than half way around it. The adhesive organs consist of a small cone of adhesive cells surrounded by a shallow epidermal cup on a long narrow stalk. A row of 4 lateral ampullae, bent at right angles, is on each side of the median row of adhesive organs. A median dorsal ampulla lies between the lateral ones, but median ampullae were not detected between the adhesive organs.

REMARKS: The species is distinguished by the spherical plant cells and sand embedded in the colourless test (the colour being conferred by the embedded material), moderately conspicuous circular systems, thick and often extensive sheet-like colonies, and large larvae. Muscles and the kink in the proximal part of the rectum resemble *Eudistoma pyriforme* Herdman, 1886 (see Hastings 1931). However, colonies of the latter species have sand grains crowded in the test, consist of pyriform lobes, and zooids have a better defined posterior stomach.

Eudistoma vittatum Kott, 1981 contain the same test inclusions as the present species but is distinguished by its relatively small upright lobes with a common basal membrane.

The syntype specimens of *Polycitor discolor* Sluiter, 1909 (ZMA TU785.1–.3) have been examined and cannot be distinguished from the present species. Although the symbiotic plant cells were reported to reach 0.8mm, none of that size was found. One of the colonies (ZMA TU785.1) has plant cells to 0.25mm in diameter, and in the others the cells are 0.1mm to 0.15mm, although in all specimens there is a wide range in their diameter. Thus, they fall well within the range recorded for *E. amplum*. Zooids of *P. discolor* also are identical with those of the present species. Zooids with the low number of stigmata (6 or 7) recorded by Sluiter were not found in the type material.

Eudistoma anaematum n.sp.

(Fig. 71a)

DISTRIBUTION

TYPE LOCALITY: Queensland (Capricorn Group, Wistari Reef, rubble fauna, coll. P. Kott 30.10.86, holotype QM GH4611; Heron I. reef, north, coll. PK 7.11.85, paratypes QM GH4610 GH4612–3).

FURTHER RECORDS: Queensland (Capricorn Group, QM G11954–7 GH4613–26; Lihou Reef, QM GH4480).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies form circular to irregular flat-topped cushions up to 2cm thick and 6cm diameter (QM GH4480), usually fixed by the whole of the lower surface. The upper surface of the colony is smooth, and openings of zooids are difficult to detect in preserved material. Zooids are arranged in circular systems of up to 5. The outer circle of branchial openings is about 3mm in diameter.

In life, colonies are shades of pinkish-beige, rose, to olive and brown (Ridgeway 1886: 'salmon-buff', 'tawny', 'ochraceus rufus', 'brick-red', 'madder-brown', 'bay', 'maroon', 'tawny-olive', 'olive'). In several colonies (QM GH4612 and GH4624) the colour shades from brick red at one end to olive at the other. When preserved the test is opaque white with a homogenous white suspension in the surface. Beneath the surface the test is cloudy-white and translucent with some minute brown pigment particles in the surface and around the zooids, although these disappear with long term preservation. Some sand is embedded in the basal part of the colony and in some specimens penetrates up into the centre. Sand is absent from the surface test. Faecal pellets are throughout. Large and conspicuous patches of pale brown to dark greenish-brown pigmented cells are in the base of the colony. The test is soft. In preservative, zooids are pinkish-beige to beige, with flecks of brownish pigment on the body wall when first preserved. The preservative stains a greenish yellow.

INTERNAL STRUCTURE: Zooids are robust, about 6mm long when partially relaxed but less than half that length when contracted. Well developed circular muscles are around each siphon, and the atrial siphons are long — at least 3 times the length of the branchial siphons. A narrow band of 3 rows of branchial tentacles is in the base of the branchial siphon. Twelve to 20 longitudinal muscle bands are on the thorax, and at least 30 transverse ones. Longitudinal muscles continue in a wide band on each side of the abdomen. The branchial sac has about 25 stigmata per row, and the first row turns anteriorly along each side of the mid-dorsal line.

The stomach, long duodenal area, posterior stomach, and well developed tubules of the gastro-intestinal gland are in the posterior end of the abdomen. A hemispherical clump of mature male follicles is in the gut loop in specimens collected in the Capricorn Group in November (QM GH4619).

Large (up to 0.8mm) embryos project out from the top of the oviducts of contracted zooids in colonies collected in October (QM GH4623), and November (QM GH4619). However, mature larvae are not in any of the available colonies.

REMARKS: *Eudistoma malum* n.sp. has the same opaque suspension in the surface test as the present species and the testis follicles are in a similar circular clump. However *E. malum* has a sandy stalk and mushroom-like colonies while those of the present species are flattened and sessile. Other sessile species (*E. muscosum* nom. nov., *E. pratulum* n.sp. and *E. purpureum* n.sp.) lack the white suspension in the surface test of preserved colonies. With the exception of *E. purpureum* n.sp., the living colonies are readily confused — the colour range found in the present species overlaps that of *E. pratulum* and *E. muscosum* nom. nov. Colour (if colonies have not been too long in preservative) is helpful in distinguishing

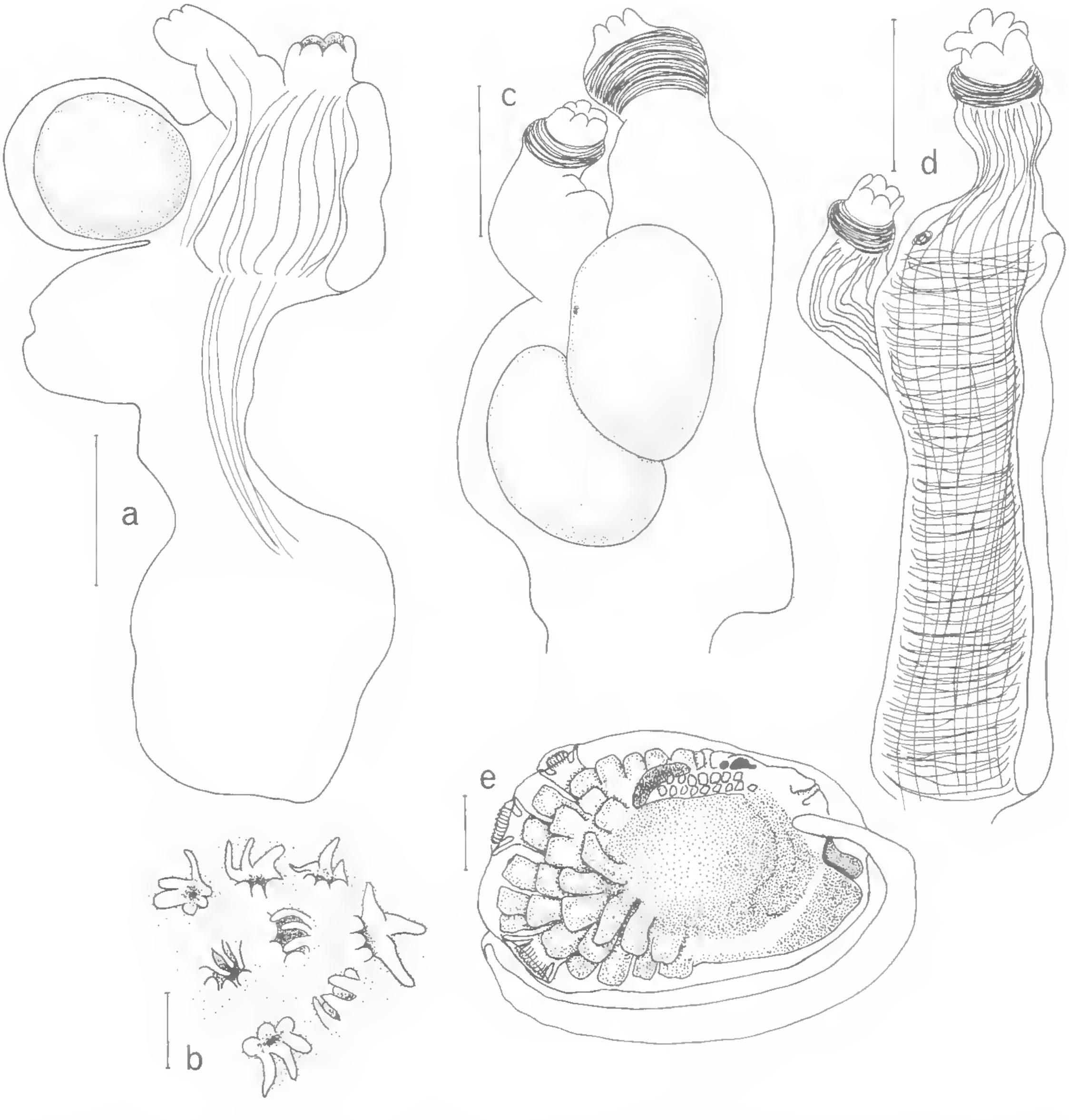


FIG. 71, *Eudistoma anaematum* n.sp. (QM GH4619): a, zooid with embryo incubating in brood pouch. *Eudistoma angolanum*: **b**, sand removed from upper surface of colony to show atrial apertures clustered together (QM GH4663); **c**, thorax showing embryos incubating and sphincter muscles (QM GH4661); **d**, thorax showing musculature (QM G11967); **e**, larva, test vesicles not shown (QM GH4661). Scales: **a–d**, 0.5mm; **e**, 0.2mm.

this species from others. Zooids are beige to pinkish-white in the present species, reddish-brown in *E. muscosum* nom. nov., and darkly pigmented in *E. purpureum*.

Embryos incubate in the oviduct as in *E. incubitum* n.sp. However they are larger than those of *E. incubitum* and are not the same spherical shape.

Eudistoma angolanum (Michaelsen, 1914)

(Fig. 71b–e)

Polycitor paesslerioides Michaelsen, 1914, var. angolanus p. 430.

Polycitor (*Eudistoma*) *angolanus* Michaelsen, 1915, p. 452.

Eudistoma angolanum: Hastings, 1931, p. 86. Millar, 1953b, p. 281; 1962, p. 162. Kott 1957a, p. 75.

Polycitor amplus: Hartmeyer, 1919, p. 105.
Eudistoma snakabri Tokioka, 1954a, p. 251.

DISTRIBUTION

NEW RECORDS: Western Australia (Houtman's Abrolhos, WAM 813.83 *QM GH2137*; Cockburn Sound, QM GH4662). Queensland (Capricorn Group, QM G11967 GH4661 GH4663-4 GH4680; Lizard I., QM G11966).

PREVIOUSLY RECORDED: Western Australia (Cape Boileau — Hartmeyer 1919, Hastings 1931; Cape Naturalist, Green Pools — AM Y1281 AM Y1203 Kott 1957a;). Tokara Is (Tokioka 1954a). West Africa (Michaelsen 1914 1915; Millar 1953b). South Africa (Millar 1962).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are flat-topped cushions up to 1cm high and 2cm or more in greatest dimension. The test is densely impregnated with sand, which also adheres to the surface of the colony. The sand is interrupted only by zooids. These lie parallel to one another, perpendicular to the upper surface of the colony.

In life the dark red of the test is seen between the sand grains. In preservative small dark pigment cells are throughout the test, especially around zooids, and the test is a dirty brown.

Up to 8 zooids are in circles of about 4mm diameter, although these are hard to see from the surface, being obscured by sand. Branchial apertures are around the perimeter of the circle, and atrial apertures open around the sides of small circular depressions (rudimentary cloacal cavities) in the upper surface. One or 2 atrial openings are also in the centre of each depression. Branchial and atrial lobes are conspicuously triangular, and dorsal lobes of the branchial aperture and anterior lobes of the atrial aperture (directing the openings away from one another) project from the surface between the sand grains.

INTERNAL STRUCTURE: In preservative zooids are pink, with a greenish stomach. They are about 0.5mm long when contracted. The siphons are both long and each one has a conspicuous bulging sphincter muscle at the outer end.

On the thorax are 20 to 25 longitudinal muscle bands and an almost complete coat of about 20 circular bands. Longitudinal muscles continue in 2 wide bands along each side of the abdomen. Three rows of fairly long branchial tentacles and 2 or 3 anterior rows of short stumpy ones are at the base of the long branchial siphon. A long pretentacular area occurs in the branchial siphon, and also a long unperforated prestigmatal area in the pharynx. About 25 stigmata are in the anterior row, but these are difficult to count. The gut has the usual long oesophageal neck, small, smooth stomach, long duodenum, and well-defined oval posterior stomach. In contracted specimens the gut is twisted posterior to the stomach.

One to 3 large embryos are in the atrial cavity of specimens collected in the Capricorn Group during October and November and in January from Lizard I. Tailed larvae are in colonies from Wistari Reef in October (QM GH4661) from Heron I. in November (QM GH4663) and from Lizard I. in January (QM G11966).

The larval trunk is 1mm long, and the tail winds about halfway around it. There are 3 rows of about 14 long ectodermal ampullae covering the anterior half of each side of the trunk. They increase in length with maturity. Larvae have red pigment in the rather prominent posterior horns of the trunk haemocoel, in the stalks of the adhesive organs, and in the ectodermal ampullae. Adhesive organs in the anterior mid-vertical line are large and have a flat-topped axial cylinder in an ectodermal cup. The larval test is crowded with vesicles, which originate as terminal expansions of fine threads that extend through the test from the ectodermal cells.

REMARKS: This species, with its hard sandy colonies and blackish red pigment showing between the sand grains has a characteristic appearance, as do the zooids, with their long, sinuous atrial siphons and bulging terminal siphonal sphincters.

The species appears related to the eastern Australian *E. reginum*, the Indian Ocean species *E. carnosum* n.sp., and the Magellanic *E. magalhaensis* Michaelsen. They all have a similar larva, with red-brown pigment in the anterior ampullae and posterior horns of the larval trunk haemocoel; and they all have well-formed systems with rudimentary cloacal cavities. *Eudistoma carnosum* n.sp. (> *Sigillina magalhaensis*: Michaelsen 1930; Kott 1957a) has the same 3 rows of larval ectodermal ampullae as the present species, although they are not as long; and its larval trunk is longer (1.5mm, but only 1.0mm in *E. angolanum*). *Eudistoma angolanum* is the only species of the group that lacks the large test vesicles and the bare (sand-free) areas over the systems of zooids. *Eudistoma muscosum* nom. nov. has similar accumulations of pigment in the posterior horns of the larval haemocoel, but is distinguished by its smooth shiny surface and lack of cloacal depressions in the surface.

Michaelsen thought the present species a variety of *Polycitor* (*Eudistoma*) *paesslerioides*. However, *P. paesslerioides* var. typicus has only weak sphincter muscles. Michaelsen (1915) subsequently elevated his var. angolanus to full species status and recognised two varieties, typica and togoensis. Millar (1953b) described a further specimen from the type location on the African Gold Coast that has characters intermediate between Michaelsen's varieties; and thus it is probable that these represent no more than intraspecific variations. The larval trunk of the Gold Coast specimen (Millar 1953b Fig. 2b) has the same rows of long papillae on the side of the larval trunk as those found in the Australian specimens.

Hastings (1931) examined the type of *Polycitor amplus*: Hartmeyer, 1919 from north-western Australia, and another large (8cm diameter and 3.5cm thick) specimen from the same location. She found the characteristic long siphons and conspicuous sphincter of *E. angolanum* in both.

The species has a wide recorded geographic range from the western African coast to the western Australian coast, and the records from the Capricorn Group and Lizard I. suggest the tropical eastern coast of Australia is included in the range. There is no known character indicating that more than a single species is involved. Unlike the strictly tropical *E. carnosum* n.sp. which has been recorded only from the Indian Ocean, records of the present species do include some from temperate waters — of both South Africa (Millar 1962) and south-western Australia (see above). This could be the explanation for the continuity of range between the West African coast and the Indian Ocean.

Eudistoma aureum n.sp.

(Fig. 72)

Eudistoma pyriforme: Kott, 1972a, p. 9.

DISTRIBUTION

TYPE LOCALITY: South Australia (St Vincent's Gulf, off West Beach *Posidonia* beds, 12-20m coll. S. Shepherd 27.12.66, holotype SAM E2084; paratypes SAM E2085).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are flat- to convex-topped lobes, up to 4cm in diameter narrowing basally where sometimes the test is produced into root-like extensions. Sand is embedded in the test throughout the lower part of the colony, and continues in a layer beneath the surface of the upper part. Thus, in the upper half of the colony, sand is absent from the surface and in the centre. The test is firm and gelatinous and the embedded sand enhances the firmness of the colony. Living colonies are reported to be bright yellow. Zooids are in circular systems.

INTERNAL STRUCTURE: Zooids are large and robust, up to 1cm long even when contracted. In preservative they are brownish-red, with irregular patches of pigment scattered in the body wall. The atrial siphon is about 3 times the length of the branchial siphon. On the thorax are about 15 strong longitudinal muscles, and these appear to subdivide, forming more numerous muscles in a wide band along each side of the abdomen. An almost continuous coat of circular muscles lies on the thorax, beneath the longitudinal bands. There is a wide band of about 6 circles of short branchial tentacles. At least 25 stigmata are in the anterior row, which curves anteriorly along

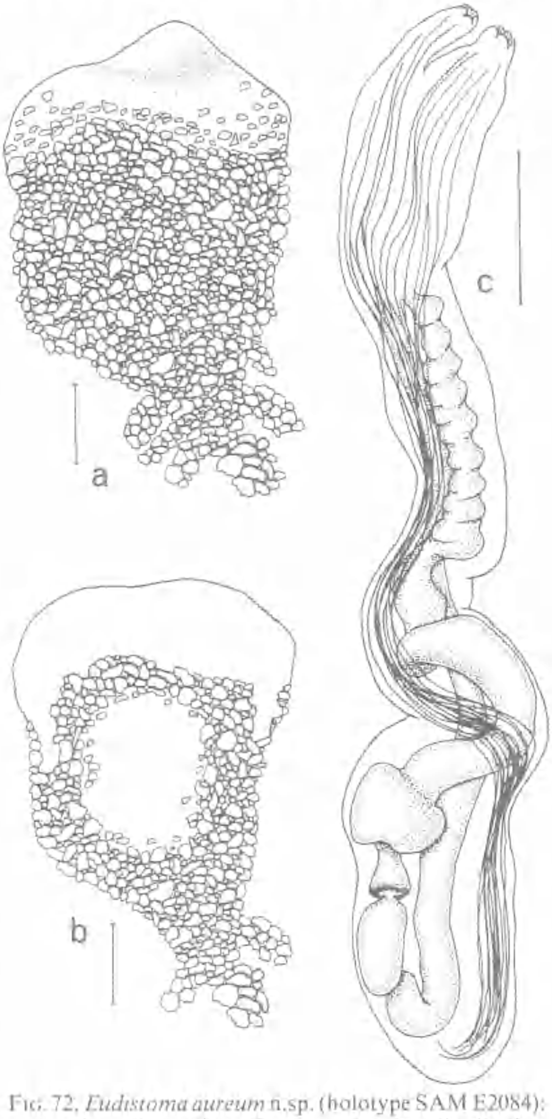


FIG. 72. *Eudistoma aureum* n.sp. (holotype SAM E2084): **a**, colony; **b**, section of colony showing distribution of sand in the test; **c**, zooid. Scales: **a**,**b**, 1cm; **c**, 1mm.

the dorsal mid-line. However, the stigmata are difficult to count in these zooids and the exact number was not determined.

The oesophageal neck is long and in these specimens is constricted into 5 more or less equal segments along its length. Since the whole abdomen is filled with trophozooite cells and there are no gonads present, it is probable that these zooids are entering the vegetative phase. The usual smooth stomach, long duodenal area, and oval posterior stomach are in the posterior part of the abdomen.

Remarks: Kott (1972a), misled by the pyriform shape of the lobes, assigned these specimens to *Eudistoma pyriforme*. However, lobes are much larger than those of *E. pyriforme*, and the naked, sand free test over the upper part of the colony further distinguishes the species, as does the bright yellow of the living specimens. *Eudistoma globosum* also has a naked sand-free layer of test over the upper surface, but is distinguished by the absence of circular systems as well as by its smaller size, the colour and the absence of a sand-free area in the centre of the upper part of the colony. The temperate species, *E. maculosum* n.sp. has a layer of sand in the middle layer of test, although the sand particles become less crowded toward the base of the colony. *Eudistoma maculosum* is further distinguished from the present species by its investing colonies and the 2-toned colour pattern of both living and preserved specimens. The general shape of the colonies, the firm test, and arrangement of zooids in the present species, resemble some of the larger specimens of the tropical *E. malum* n.sp. (see QM GH798). The latter species also has sand embedded in the stalk, but lacks the characteristic layer of embedded sand beneath the upper surface.

Eudistoma bulbatum n.sp.

(Fig. 73)

Eudistoma pyriforme Kott, 1972d, p. 244.

Distribution

Type Locality: New South Wales, off Cronulla, 140m, coll. J. MacIntyre 16.6.65 holotype AM Y2204; paratypes AM Y835 Y842 Y1120. The species is known only from the type locality.

Description

External Appearance: Colonies are upright and club-shaped, the lower half swollen, sometimes with some fine basal root-like extensions, and often divided. They are up to 2.5cm high, the upper third of the colony about 0.5cm in diameter, and the lower two thirds about 1cm in

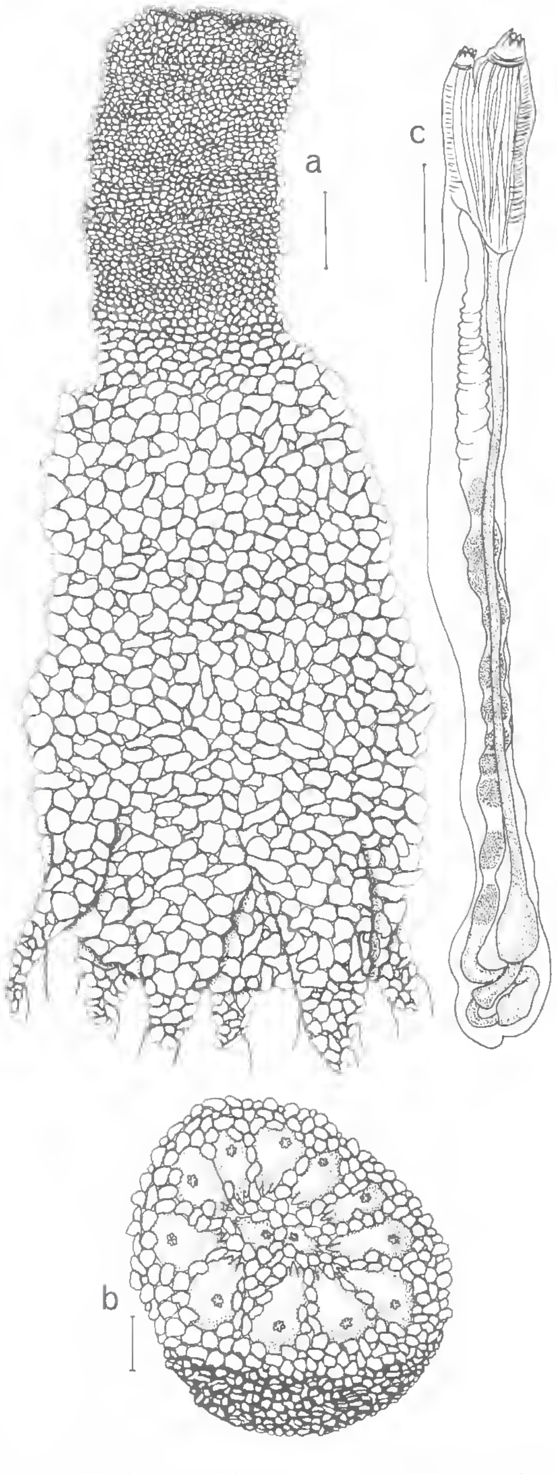


Fig. 73, *Eudistoma bulbatum* n.sp. (paratype AM Y835): **a**, colony; **b**, upper surface of colony showing openings, atrial apertures directed in toward the centre; **c**, zooid. Scales: **a**, 2mm; **b**,**c**, 1mm.

diameter. The test is sandy throughout. The lower swollen part of the colony apparently was embedded in a sandy substrate and has larger particles of sand adhering to the outside of the colony than are embedded in the test.

Zooids are in a circle around the narrow upper part of the colony. The test is raised over the anterior end of each zooid. Branchial apertures are around the outer perimeter, and atrial apertures around a central depression. One or 2 zooids are sometimes in the centre of the circle with their atrial apertures directed out toward the atrial apertures of the circle of zooids surrounding them. Each colony has about 12 zooids.

Internal Structure. Zooids are robust and muscular. On the thorax are about 20 longitudinal muscles and an almost continuous inner coat of circular muscles containing at least 40 bands. The abdomen is almost completely encased by the longitudinal muscles which continue along each side in a very wide band. In these specimens the zooids are about 1cm long, and are found contracted into the base of the colonies.

The branchial aperture is terminal, but is turned toward the outside of the colony, and its dorsal lobes are longer than the ventral ones. The atrial siphon arises from the antero-dorsal part of the thorax and is not longer than the branchial siphon. The two apertures are well separated by the ventral inclination of the branchial siphon and the antero-dorsal part of the zooid stretched out between them. Lobes of the apertures are large and triangular.

An extensive prebranchial region exists behind the 3 rows of tentacles. About 15 stigmata are in the anterior row, which curves anteriorly alongside the mid-dorsal line, although contraction makes them impossible to count precisely. The rectum of the contracted zooid is finely wrinkled and the proximal part of the ascending limb of the gut is bent up in a loop posterior to the stomach. The stomach, duodenal area, and posterior stomach are in the posterior end of the abdomen. The stomach is dark greenish-yellow. Neither gonads nor embryos are in the available material.

Remarks. The free-standing club-shaped colonies of the species are distinctive. A colony most closely resembles one of the almost cylindrical upright lobes of *E. loricatum* (Sluiter, 1909) which has the same small, simple circular systems of zooids. However *E. loricatum* has no sand around the upper part of the colony, each lobe is much smaller, and is attached with others to a common basal test mass.

Eudistoma carnosum n.sp

(Fig. 74)

Polycitor (*Eudistoma*) *paesslerioides*: Michaelsen, 1919, var. hupferi p. 73 (part, material from the Seychelles and Red Sea with cloacal systems.

Sigillina (*Paessleria*) *magalhaensis*: Michaelsen, 1930 p 492 (part, material with cloacal systems).

Sigillina magalhaensis: Kott, 1957a, p. 79.

Distribution

Type Locality. Western Australia (Rottnest I. Cape Vlamingh, Fish Hook Bay, under undercut of limestone reefs, coll. P. Kott 19.11.51, holotype AM Y1289; Rottnest I. Geordie Bay, paratype AM Y1291; Rottnest I., Mary Cove coll. P. Kott November 1951, paratype AM Y1290).

New Records. Western Australia (Houtman's Abrolhos, WAM 383.75 814.83 *QM GH2108*; Rottnest I., QM GH4659 GH4660).

Previously Recorded. Western Australia (Houtman's Abrolhos — Michaelsen 1930; Cockburn Sound — Michaelsen 1930, AM Y2205 Kott 1957a).

Description

External Appearance. Colonies form robust sandy, flat-topped cushions, up to 5cm long, 4cm wide and 2cm high. Sometimes the surface is divided by sandy ridges into circular areas, about 2cm in diameter with a central, conical prominence and terminal cloacal aperture. Systems are 3 to 6mm in diameter and contain up to 20 zooids. Branchial apertures are on the outer surface of the colony, and atrial apertures are around the sides and in the floor of the cloacal cavities that lie in the centre of each system. Sand is absent from the surface test around the cloacal cavity and usually it does not adhere to the outside of the colony. Anterior lobes of the atrial aperture and dorsal lobes of the branchial aperture are enlarged and, with their covering of test, project around the openings. The pointed anterior atrial lobes are especially conspicuous and form the rim of the cloacal cavity.

The colour of the living colonies is not known. Large spherical vesicles 0.3 to 0.5mm in diameter, are throughout the test, except where the embedded sand excludes them. These vesicles contain crystalline particles.

Internal Structure. Zooids are large, about 0.5cm long when contracted. Apertures are on long siphons with a narrow sphincter muscle near the end of each siphon. The thoracic musculature is strong with about 30 longitudinal bands, and the circular horizontal muscles form an almost continuous coat of about 30 bands beneath the longitudinal ones. The longitudinal muscles continue along the abdomen in about 2 wide bands on each side. About 20 moderately long branchial tentacles are in 3 rows and some stumpy ones

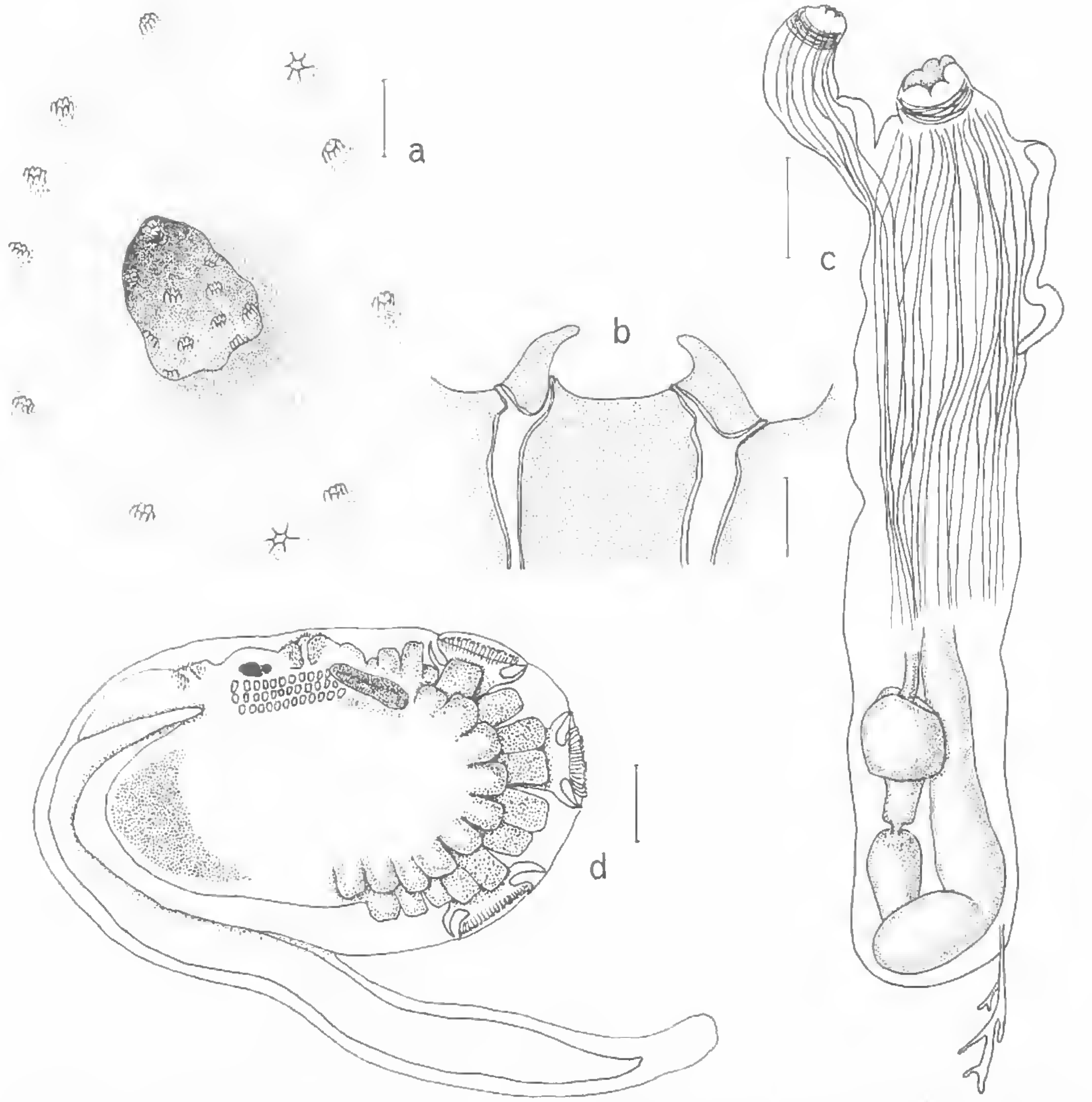


FIG. 74. *Eudistoma carnosum* n.sp.: **a**, surface view of colony showing branchial openings of a system, with atrial openings in a rudimentary common cloaca (holotype AM Y1289); **b**, section through system showing zooid openings (semidiagrammatic); **c**, contracted zooid with muscles removed from posterior half of abdomen (holotype AM Y1289); **d**, larva showing pigment in posterior horn of left haemocoele and pointed extensions of ectodermal cells around apertures, but test vesicles not shown (WAM 814.83). Scales: **a**, 1mm; **c**, 0.5mm; **d**, 0.2mm.

are little more than papillae in anterior rows, but these could not be counted. There are about 16 stigmata per row. The dorsal stigmata of the anterior row on each side curve anteriorly along each side of the dorsal mid-line.

The abdomen is of the usual form with a long, narrow oesophageal neck. At the posterior end of the descending limb of the gut loop is a rather flabby and inconspicuous posterior stomach.

The rather large (1mm diameter) eggs are dark red-brown in preservative. Zooids of a specimen collected from Houtman's Abrolhos in August (WAM 814.83, *QM GH2108*) have a tailed larva in the atrial cavity. The trunk is 1.5mm long and the tail reaches only to its anterior end. A feature of the larva is the numerous ampullae arranged in 2 rows of about 14 on each side of the median adhesive organs. The adhesive organs have wide axial columns and are on short, wide stalks. There are 3 rows of stigmata. Spikey processes from the ectoderm around the apertures extend out into the test. Brown pigment is in the posterior horns of the larval trunk haemocoel and in the stalks of the adhesive organs.

Remarks: Large cloacal cavities in their conspicuous sand-free area of test are characteristic of the species. It is distinguished from *E. reginum* by its larger colonies and cloacal systems, longer siphons, large larval trunk with more numerous ectodermal ampullae and larger test vesicles.

Michaelsen (1919, 1920) assigned specimens from the Seychelles and questionably also from the Red Sea to the western African variety hupferi of the species *Polycitor* (*Eudistoma*) *paesslerioides* (Michaelsen 1914). Subsequently (1930), he placed the Seychelles and Red Sea material with newly recorded specimens from Western Australia in synonymy with the species *Polycitor magalhaensis* Michaelsen, 1907 from the Magellanic region, as *Sigillina* (*Paessleria*) *magalhaensis*. *Sigillina* (*Eudistoma*) *paesslerioides*, represented by varieties hupferi and typicus from West Africa, was distinguished from *S.* (*Paessleria*) *magalhaensis* by its smooth stomach and more numerous (more than 100) branchial tentacles (Michaelsen 1930). The stomach folds that Michaelsen believed characteristic of the subgenus *Sigillina* (*Paessleria*) are artefacts and not true stomach folds, and the division of *Eudistoma* into the subgenera that Michaelsen proposed is invalid. Nevertheless the West African and Indian Ocean specimens appear separate species, their separation valid on morphological (more numerous branchial tentacles: Michaelsen 1930) as well as geographic grounds. Only some of Michaelsen's western Australian and Seychelles colonies (those with cloacal systems) are identical with the newly recorded material.

The Magellanic species, with similar cloacal systems and large embedded vesicles (symbiotic cells?) appear closely related to the Indian Ocean ones. It is unlikely they are conspecific because they have stalked colonies with a rounded head and much longer zooids, rather than the platform-like irregular and sessile colonies of the Australian specimens for which the present new species is erected.

Eudistoma carnosum n.sp. resembles *Eudistoma angolanum* Michaelsen, 1915, which, like the present species, was described originally as a variety of *Polycitor* (*Eudistoma*) *paesslerioides* Michaelsen, 1914. *Eudistoma angolanum* is distinguished by its conspicuous band of circular muscles on each of the siphons (see above).

The spikey ectodermal processes around the apertures were observed also in *Eudistoma ovatum*, and may occur also in other species (see Annotated Glossary: **larvae**).

Eudistoma constrictum n.sp.

(Fig. 75, Plate 15b)

Distribution

Type Locality: South Australia (Great Australian Bight, Yorke Peninsula, low water mark under rocks on headland near Chinamen's Hat I., coll. N. Holmes 6.11.76, holotype SAM E2083; Investigator Group, Topgallant I., bottom of rock slope near cliffs 7m, coll. N. Holmes 10.4.83, photo index PE0047/R929, paratype QM GH2291; Avoid Bay, Golden I, coll. N. Holmes 9.4.87, paratype QM GH4186).

Further Records: South Australia (Great Australian Bight, QM GH2406; Yorke Peninsula, SAM E2087; West I. QM GH2403; Spencer Gulf, QM GH4551).

Description

External Appearance: Colonies are irregular rounded cushions of maximum dimension 4cm and up to 1cm high. The upper surface slightly overlaps the base. Zooids open on the upper surface by separate branchial and atrial apertures that are placed fairly close to one another in an oval sand-free area. Sometimes the test between zooids is crowded with sand particles and faecal pellets. The sand gradually becomes less crowded toward the base. Sand is not always present in the upper half of the colony, although the oval areas in the surface are quite conspicuous — the solid layer of test between zooids contrasting with the thin layer over the top of each zooid.

Each zooid is contained in a compartment in the test which is constricted around the upper part of the oesophageal neck to form a narrow canal between the roomy abdominal and thoracic cavities. Frequently the contracted zooids are severed at this point leaving the thorax behind in the upper layer of the colony as the abdomen contracts back into the base. The sand embedded in the test makes the compartments rigid. Zooids extend at angles to one another in the test, crossing one another irregularly.

Internal Structure: Zooids are robust and muscular. They are pinkish-brown in alcohol preservative. About 30 longitudinal muscle bands are on the thorax. More numerous circular ones are irregularly distributed and confined to the middle of the thorax. Longitudinal muscles continue onto the abdomen in 4 wide bands on

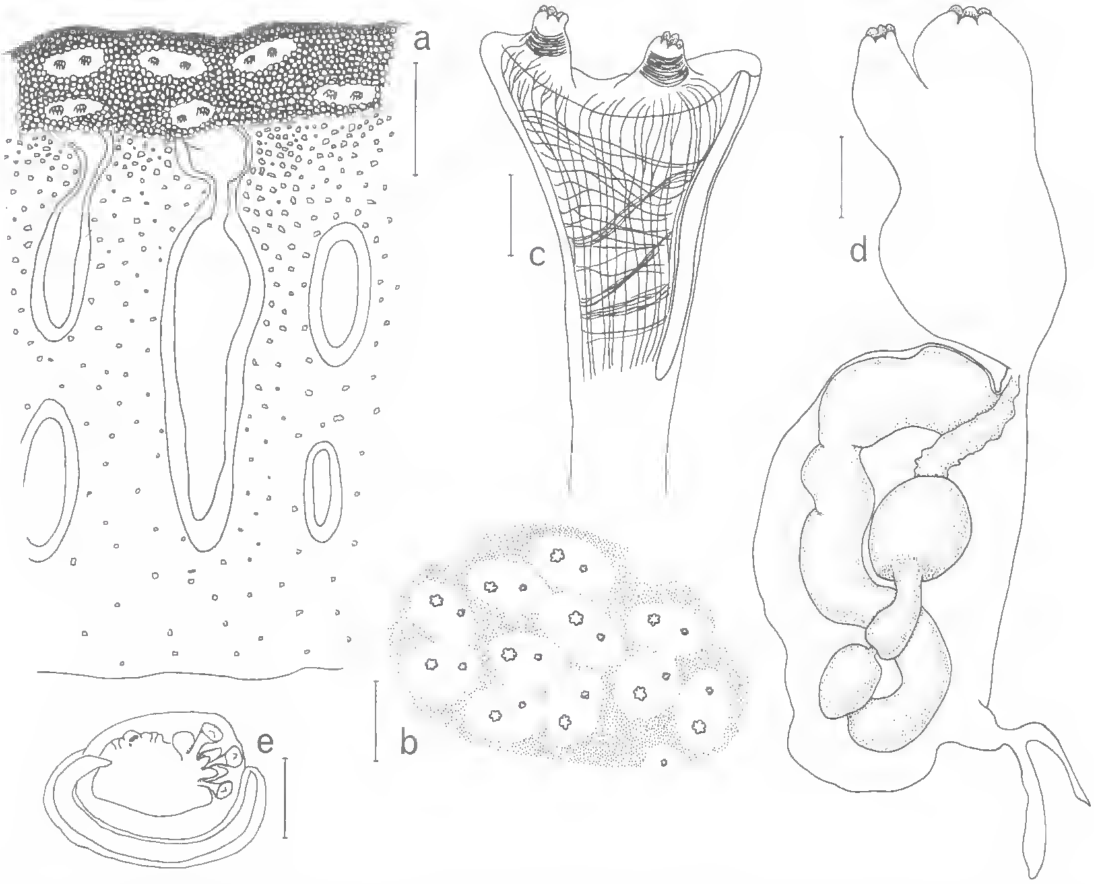


FIG. 75, *Eudistoma constrictum* n.sp.: **a**, section through colony showing zooids opening on the surface in sand-free areas (paratype QM GH2291); **b**, zooid openings on surface of colony (holotype SAM E2083); **c**, thorax showing muscles (paratype QM GH4186); **d**, whole zooid showing gut loop (paratype QM GH2291); **e**, larva (paratype QM GH4186). Scales: **a,b**, 2mm; **c–e**, 0.5mm.

each side. Both siphons are relatively short. The anterior end of the zooid is often flattened, with both apertures rising from the flat anterior surface. Short branchial tentacles are arranged in about 7 rows at the base of the branchial siphon. There are about 25 stigmata per row, but these were difficult to count. The dorsal end (involving about 5 stigmata) of the anterior row curves forward along each side of the dorsal mid-line. A short oval posterior stomach is in the descending limb of the gut loop.

Up to 4 embryos are present in the peribranchial cavity of specimens collected in April (QM GH418). Larvae have a trunk about 1mm long with the tail wound about three quarters of the way around it. Lateral as well as median ampullae alternate with the adhesive organs.

REMARKS: This species has a smooth, sandy surface, and sand is present throughout the test as in *E. ovatum* and *E. sabulosum* n.sp. It is readily distinguished by the oval sand free area of thin test over the anterior end of each zooid, the absence of circular systems, and the narrow constriction of the test between the abdominal and thoracic test cavities. In *Polycitorella* spp. there is a similar constriction, containing a sphincter which regulates the withdrawal of the zooids from the surface. However, in *E. constrictum* a similar circular muscle is not present in the constricted part of the test.

The absence of systems is a relatively rare occurrence in *Eudistoma*, known only in the present species, *E. microlarvum* n.sp. and in the stalked species *E. globosum*, *E. elongatum* and *E. laysani*. In most others, zooids are arranged in rudimentary systems.

Eudistoma eboreum n.sp.
(Fig. 76a,b)

DISTRIBUTION

TYPE LOCALITY: Queensland (MacGillivray's Reef near Lizard I., 14m, coll. D. Phillips June 1980, holotype QM GH336).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype is the only specimen available. It is a large sessile cushion, convex on the upper surface, about 3cm in diameter and 1cm thick in the centre. The upper surface is smooth and rounded. In life it was reported 'whitish'. In preservative it is firm, slightly translucent and pinkish-buff with spherical to oval brownish-orange pigment cells, about 0.01mm in diameter, distributed fairly evenly through the test. Large, black fusiform to branched, dendritic cells are also in patches, especially around the zooids. Zooids themselves are whitish in preservative with some white patches in the body wall.

There are circular systems of 3, 4 or 5 zooids. Atrial apertures are fairly close together in the centre of the triangle, rectangle or circle outlined by the branchial apertures. Branchial apertures are well separated from one another, and zooids are not crowded.

INTERNAL STRUCTURE: Zooids are robust, about 1cm long when partially contracted. The atrial siphon is long and often expands into a balloon-like structure. A discrete sphincter muscle is around the distal end of the atrial siphon and around the short branchial siphon. About 20 longitudinal thoracic muscles overlie an almost continuous coat of circular muscles and then extend along the abdomen in a wide band on each side. About 20 stigmata are in each of the 3 rows, although the exact number was not determined. The anterior row, projecting forward along each side of the mid-dorsal line has more stigmata than the others.

The oesophageal neck is long. The stomach, long duodenum and small oval posterior stomach are at the posterior end of the descending limb of the gut loop. Gonads in the gut loop at the posterior end of the abdomen are mature. A large (1mm long) embryo is in the atrial cavity.

REMARKS: Larvae are not known, but the size of the embryos present in the atrial cavity of the holotype indicates the larval trunk would be more than 1mm. The known species with larvae of this size, gelatinous smooth-surfaced test without embedded sand, and a sessile habit are *E. purpureum* n.sp. and *E. muscosum* nom. nov. Neither of these have the distinctive dendritic cells of the present species. It is further distinguished by its especially long atrial siphons and sparse zooids.

Eudistoma elongatum (Herdman, 1886)
(Fig. 76c–f. Plate 15c)

Colella elongata Herdman, 1886, p. 110. Herdman and Riddell, 1913, p. 882.
Eudistoma elongata: Kott, 1957a, p. 78.

DISTRIBUTION

NEW RECORDS: New South Wales (Jervis Bay, QM G10037). Queensland (Moreton Bay, QM G4906 G4910 G4966–7 G10047 G10147 GH356 GH4528–9: Fraser I., QM GH4527; Hervey Bay, QM G11938).

PREVIOUSLY RECORDED: New South Wales (Port Hacking, Port Stephens — AM G12945 G12952 U3937 Y1277 Kott 1957a; Newcastle Bight and Crookhaven River — AM Y12199 Y12200 Herdman and Riddell 1915; Port Jackson — Herdman 1886). Queensland (Currumbin — Kott 1957a; Moreton Bay — AM U3933 Y2167 Kott 1957a).

The species is common in muddy habitats and on wharf piles in protected waters over the whole of its range.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of numerous club-shaped to long (up to 60cm) cylindrical, rope-like zooid-bearing heads about 0.5cm in diameter, on short cylindrical stalks of almost the same diameter as the head. In life they are opaque, whitish to iridescent blue. Occasionally they remain more or less the same colour in preservative, but more often become a brownish-pink with soft transparent test. Faecal pellets are in the test, but embedded sand is not.

Zooids are crowded in the head, opening all around the surface. Atrial and branchial apertures of each zooid open fairly close together, the atrial aperture anterior to the branchial opening. Systems are not formed.

INTERNAL STRUCTURE: Zooids are small, up to 3mm long when contracted. The siphons are relatively short. About 20 longitudinal muscle bands are on the thorax forming a rather open meshwork with a similar number of transverse bands. Separate longitudinal muscles continue along each side of the ventral mid-line of the abdomen, and are not collected into bands. Stigmata are about 20 per row. Zooids have the usual long oesophageal neck with the small smooth stomach near the posterior end of the abdomen. Gonads are in the posterior end of the gut loop. A small oval posterior stomach is in the posterior end of the descending limb of the gut loop.

Up to 8 embryos are in the atrial cavity of colonies collected in January and April, only 2 in those collected in July and October, and none

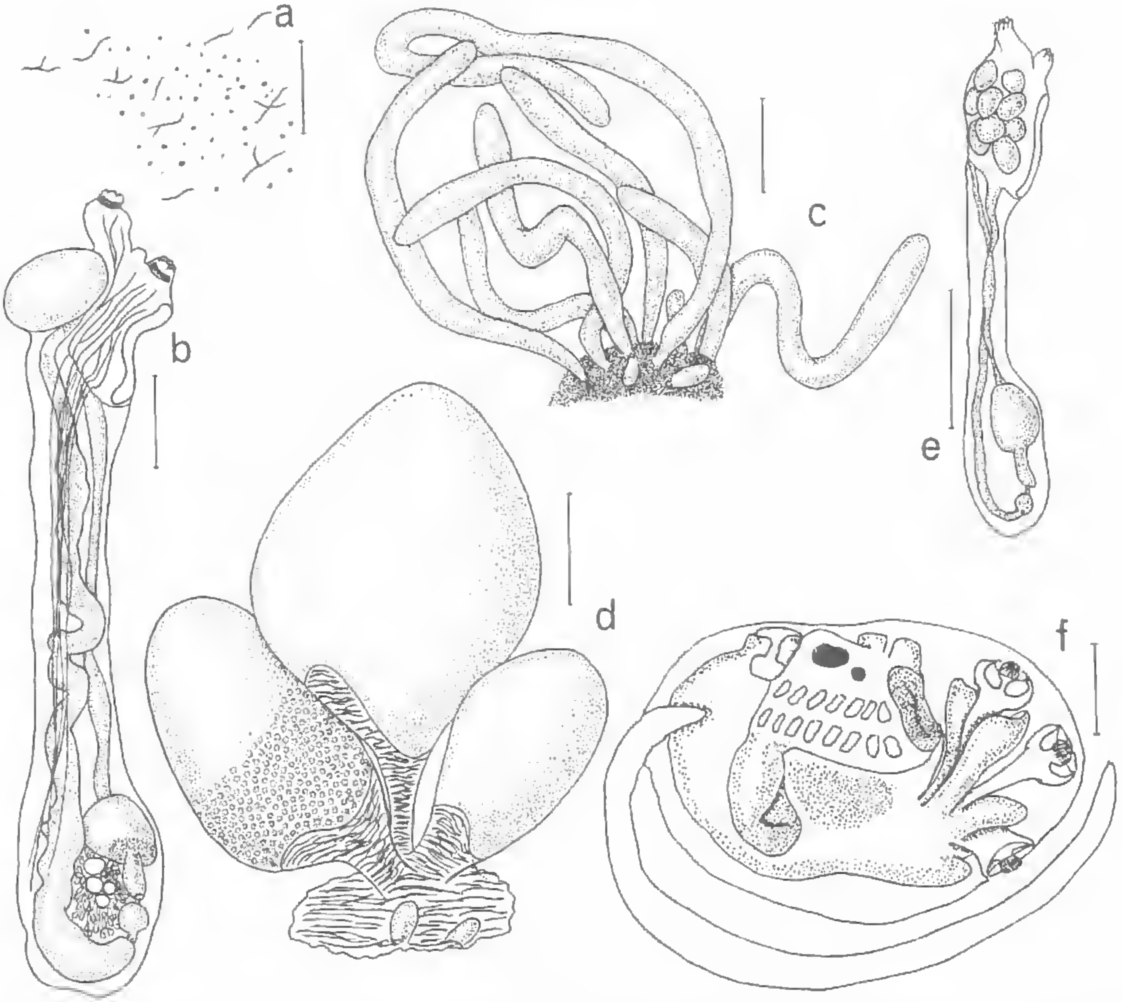


FIG. 76, *Eudistoma choreum* n.sp. (holotype QM GH336): **a**, portion of test showing pigment cells; **b**, zooid. *Eudistoma elongatum*: **c,d**, colonies (QM G4806 GH4527); **e**, zooid, contracted, showing embryos packed in atrial cavity (AM Y1277); **f**, larva (AM Y1277). Scales: **a**, 0.5mm; **b,e**, 1mm; **c**, 2cm; **d**, 1cm; **f**, 0.1mm..

in colonies collected in May, August and December.

Larvae are small with a trunk 0.5mm long. The tail reaches only to the anterior end of the trunk. There is an ocellus and an otolith. Four large ectodermal ampullae alternate with the stalked adhesive organs in the median line.

REMARKS: The long stalked heads of this species are unusual in this genus. Specimens are softer and more flexible than *Sigillina australis* which has similar long cylindrical heads. Some degree of overlap exists between smaller colonies of this species and some larger ones of *Eudistoma laysani*, and the species may be related — *E. elongatum* being an indigenous species with its range confined to protected waters in the northern half of the New South Wales coast to southern Queensland. *Eudistoma elongatum* can be distinguished from *E. laysani* by its more numerous thoracic muscle bands, longer zooids, and more numerous embryos in the atrial cavity, as well as the much longer zooid-bearing heads.

Eudistoma gilboviride (Sluiter, 1909)
(Fig. 77. Plate 15d–f)

Polycitor gilboviridis Sluiter, 1909, p. 6.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM G10043 GH4593; Swain Reefs, QM G11961; Lizard I., QM G11959; Britomart Reef, QM GH4530).

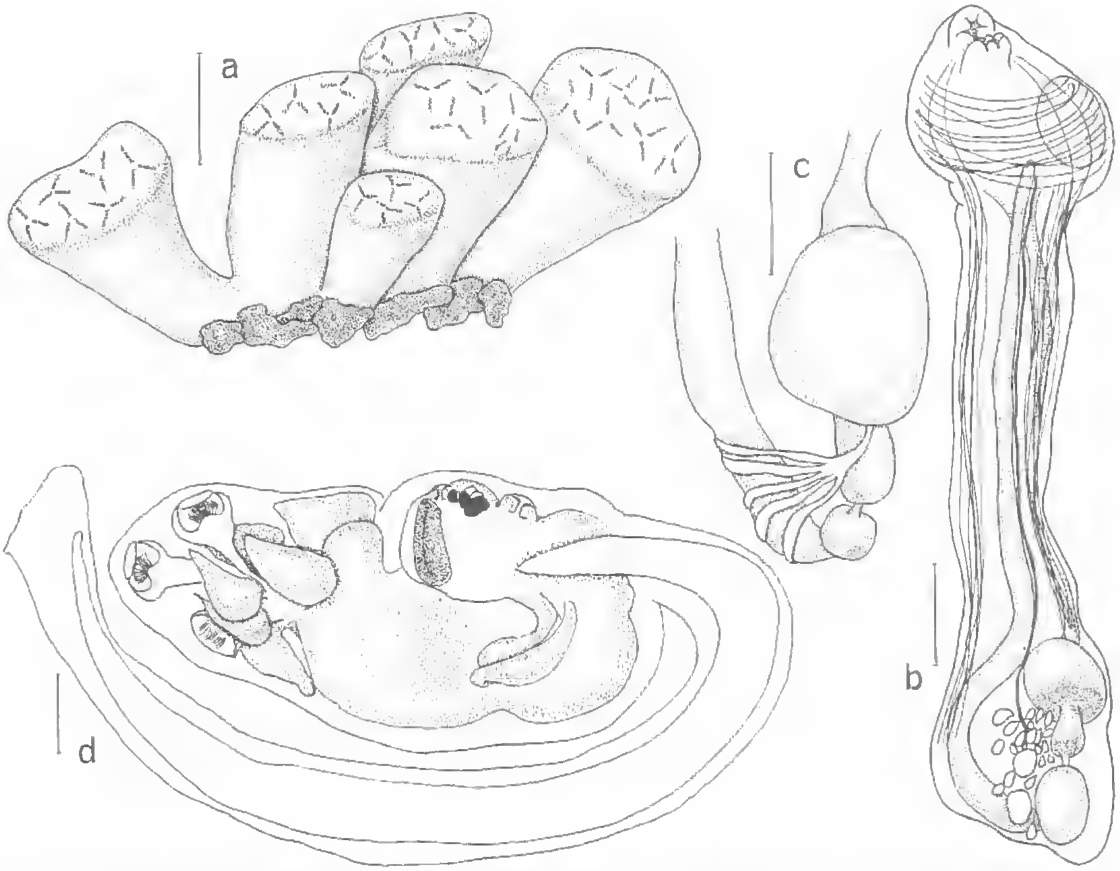


FIG. 77. *Eudistoma gilboviride*: a, colony (QM GH4530); b, zooid (QM GH4530); c, gut loop with branches of gastro-intestinal gland (QM G11959); d, larva (QM GH4530). Scales: a, 1cm; b,c, 0.5mm; d, 0.1mm.

PREVIOUSLY RECORDED. Indonesia (ZMA TU1269 Sluiter 1909).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of small (2cm high), crowded, wedge-shaped lobes, widest on the upper flat surface (up to 1.5cm diameter) and reducing in diameter toward the base where they are joined to common basal test. The test is firm and gelatinous and zooids open into slightly depressed areas on the upper surface.

In life the newly recorded colonies are reported as green base with dark green lobes mottled cream, green and yellow, or grey-green. In living colonies lobes are inflated and appear confluent. Freshly preserved specimens are greenish-black, with the pigment in minute cells in the surface test around, but not in zooids. Beneath the surface layer the test is greenish grey, and rather transparent with sparsely scattered dark pigment cells. Zooids are pinkish-brown to white. Some sand occurs in the base of the colony and it extends up into the centre of each lobe. Long-preserved specimens are grey, with black pigment cells crowded around and over zooids resulting in blackish surface marks emphasing the arrangement of zooids. In the type specimen (ZMA TU1269) the colour pattern shown by Sluiter (1909) is still recognisable, demonstrating the unusual stability of pigments in this species. The type differs from the newly recorded material in having yellow pigment in the raised swellings of solid test between the depressions and furrows into which zooids open. Depressions are made conspicuous by the concentration of dark pigment always found associated with zooids in this species.

Zooids all open on the flat upper surface of each lobe. In small diameter lobes they are in a circle just inside the outer margin of the upper surface. As the lobes increase in diameter 2 or 3 zooids form small systems with their atrial apertures close together, and sometimes a few zooids seem not part of a circular arrangement.

Internal Structure: The zooids are about 4mm long when contracted, and not particularly muscular. The atrial siphon is longer than the branchial siphon. Muscle bands are fine, about 14 longitudinal crossing about 20 circular bands on the thorax to form a rather open mesh. Longitudinal muscles extend along the ventral side of the abdomen, one band each side of the mid-ventral line. When contracted they draw up the ventral part of the abdomen causing the proximal part of the rectum to curve out. Sometimes the whole posterior end of the gut is bent up against the rest of the abdomen.

Stigmata are reduced in length toward the ventral end of each row. The anterior row has 24 stigmata, the dorsal 4 turning anteriorly along the mid-dorsal line, the middle row 20 and the posterior row 18. There are 3 rows of branchial tentacles. The large, oval, posterior stomach is in the posterior end of the gut loop. The gastro-intestinal gland has long tubules curving around the rectum.

Testis follicles are not crowded. One or 2 embryos are in the atrial cavity of specimens taken from Lizard I. in November. In the colony from Britomart Reef (QM GH4530) are 2 embryos, one immature and the other a tailed larva. The larval trunk is large (0.9mm long), and the tail curves up across the left side of the anterior end of the trunk and over the upper surface. The paired, lateral, ectodermal ampullae are large and leaf-shaped extending anteriorly and terminating in a point. They are dorsal and ventral to the adhesive organs, and alternate with them. The ventral pair have an unusual rounded prominence at the posterior end.

Remarks: Small, flat-topped and wedge-shaped lobes of the colonies and dark pigment cells that persist in the surface test after preservation are distinctive, as is the rather sparse distribution of zooids, the small systems, and leaf-shaped ampullae of the larvae. In *E. glaucum* numerous lobes arise from common basal test but they are a different colour and are larger and more rounded. They cannot be confused with colonies of the present species.

Eudistoma glaucum (Sluiter, 1909)

(Fig. 78)

Polycitor glaucus Sluiter, 1909, p. 12.

Eudistoma glaucus: Tokioka and Nishikawa, 1975, p. 331.

Eudistoma rigida Tokioka, 1955b, p. 50. **Not** Kott, 1981, p. 152 (< *E. tigrum* n.sp.); *Eudistoma rigidum*: Monniot and Monniot, 1987, p. 70 (? < *E. muscosum* nom. nov.).

? *Eudistoma olivaceum*: Monniot and Monniot, 1987, p. 67. **Not** Van Name 1902, p. 120.

Distribution

New Records: Queensland (Capricorn Group, QM G11952 G11962-5 G11979 GH3005 GH4119 GH4426-31 GH4441 GH4452 GH4468; Swain Reefs, QM GH4469; Broadhurst Reef, QM GH4425; Little Mary Reef, GH279).

Previously Recorded: Palau Is (Tokioka 1955b), Indonesia (Sluiter 1909), Okinawa (Tokioka and Nishikawa 1975), Fiji (Kott 1981).

Description

External Appearance: Colonies consist of large (up to 3cm diameter) rounded or cushion-like heads, usually with a short thick, basal stalk. Often several heads of various sizes arise from a common basal mass. The surface of the colony is smooth and shiny. The test is gelatinous and firm. Living specimens are a vivid, deep, moss-green becoming blackish-blue in preservative. The pigment leaches into the preservative and although some minute dark pigment cells persist, they disappear in time from the colony. Sometimes zooids are green when first preserved, with the pigment especially retained in the gut, gonads and body wall. In due course pigment is lost altogether from preserved zooids. The test contains some sand, especially in the stalk and in the centre of the colony but usually it is absent from the softer test of the heads of the colony. Faecal pellets are also present in the test and often are coloured green. Zooids are arranged in small circular systems of 4 or 5 zooids with their atrial apertures in the centre of the circle.

Internal Structure: Zooids are robust and long, even contracted ones being up to 1cm long. However, in comparison with zooids of some other species (eg. *E. anaematum* n.sp., *E. purpureum* n.sp. and *E. pratulum* n.sp.) both the thorax and the atrial siphon are relatively short. About 20 fine longitudinal muscle bands are on the thorax, and these extend along each side of the abdomen. More numerous (about 50) inner circular bands are evenly spaced on the thorax and around the branchial and atrial siphons. Twenty long rectangular stigmata are in the posterior row and 25 in the anterior row, which has its dorsal end curving forward along each side of the mid-line. Extensive pre- and post-stigmatal regions are in the pharynx. The oesophageal neck is long and thin. Gonads are in the gut loop and testis follicles spill out over its sides. There is a rather indistinct posterior stomach. A delicate but relatively long vascular appendix projects from the posterior end of the zooid.

In the newly recorded material embryos (one

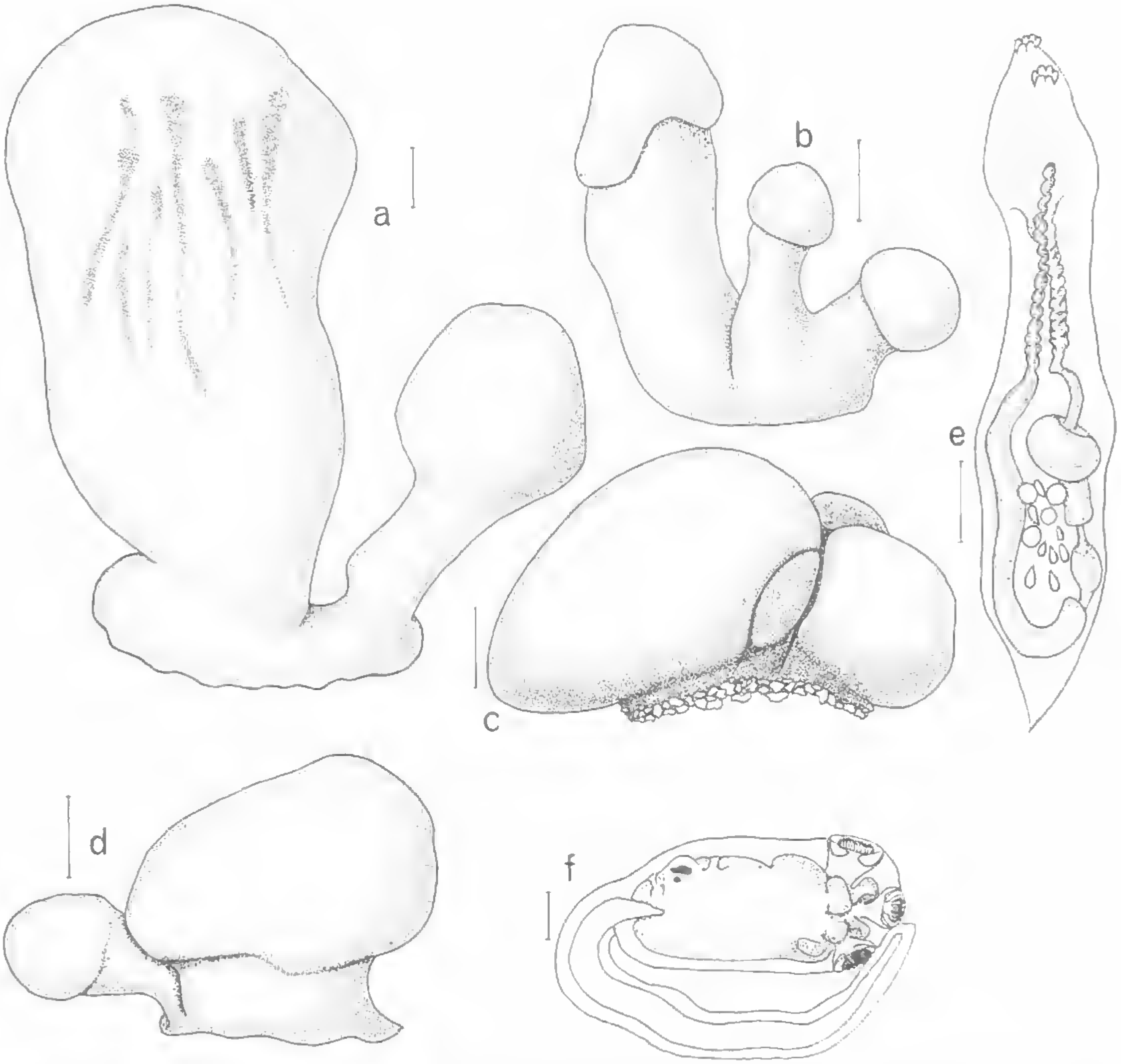


FIG. 78. *Eudistoma glaucum*: **a**, colony (QM G11962); **b–d**, outlines of various colonies (QM G11952 G11962 G11979); **e**, zooid (QM G11979); **f**, larva (QM G11979). Scales: **a**, 2mm; **b–d**, 1cm; **e**, 0.5mm; **f**, 0.2mm.

or 2) are in the atrial cavity of colonies taken from the Capricorn Group in December and January (QM G11963 G11979), but not in those collected in March, July or September. The larval trunk is about 1.2mm long.

The adhesive organs are in a median vertical row anteriorly. They have short thick stalks and vertically elongated axial platforms of columnar cells in shallow epidermal cups. The adhesive organs alternate with epidermal ampullae in the mid-line, and 3 lateral accessory ampullae are on each side, one more or less on each side of the base of each adhesive organ.

REMARKS: Tokioka and Nishikawa (1975) concluded that *Eudistoma rigida* Tokioka, 1955b from the Palau Is, with its green test, but yellowish-brown rather than green zooids, was distinct from the present species. However, zooids and colony of both species resemble one another, and in preservative become the same bluish-black. They are here considered synonymous. *Eudistoma marianense* Tokioka, 1967a has a similar colony and larva, although the larval trunk is slightly longer than that of the present species. The colour of the Marianas Is specimen is not recorded. The present species is never the red-brown colour of the small colonies assigned to *E. rigidum* by Monniot and Monniot (1987).

Eudistoma viride Tokioka, 1955b, from the Palau Is has its green pigmentation principally in the zooids, and they can be seen through the translucent test, while the whole test is green and opaque in the present species. *Eudistoma viride* also has relatively large zooids and an incubatory pouch. It appears to be a synonym of *Sigillina signifera* (see above). Tokioka and Nishikawa (1975) have discussed the relationship of *E. tokarae* Tokioka, 1954a from the Tokara Is, with the present species. Their view that the former species represents juveniles of *E. glaucum* seems unlikely since *E. tokarae* has a milky white translucent test, while the principal characteristic of the present species is its opaque test, green when living and blackish blue in preservative.

The colour of the colony and the distribution of pigment in *E. glaucum* resembles that in *E. olivaceum* (Van Name, 1902) from the tropical Atlantic. Specimens of the latter species from the Bahamas have a variety of colony forms, some with sessile heads on a basal mat and some long and stalked (AMNH349; see also Van Name 1945). Although some resemble the shape of colonies of the present species, heads are smaller with fewer zooids and stalks are longer. Further, it is unlikely that the tropical Atlantic species has a range that includes the western Pacific. Therefore, the two should not be regarded as conspecific. Monniot and Monniot (1987) refer to a specimen (undescribed) of *E. olivaceum* from Fiji, but it probably belongs to the present species.

The posterior abdominal vascular stolon of this species is longer than in most others of the genus. It extends down into the stalk as in *Sigillina* spp., but lacks the extension of the epicardium which occurs in the latter genus. *Eudistoma superlatum* n.sp. has a similar vascular stolon

Eudistoma globosum Kott, 1957
(Fig. 79a–d)

Eudistoma globosum Kott, 1957a, p. 72

DISTRIBUTION

NEW RECORDS: Western Australia (Houtman's Abrolhos, WAM 832.83 839.83; Rottnest I., QM GH4563, WAM 133.75; Margaret River, WAM 815.83 (*QM GH2128*). Queensland (Capricorn Group, QM GH4579)

PREVIOUSLY RECORDED: Western Australia (Rottnest I. AM Y1212 Y1270 4 Kott 1957a).

DESCRIPTION

EXTERNAL APPEARANCE. Colonies usually consist of rounded to oval or conical heads that overlap a short, thick stalk. Stalked heads are up to 4cm high. Several heads sometimes arise from basal test, or the stalk may branch. The surface test of the head of the colony is always free of sand. However, sand grains are crowded in the test and project up from the stalk into the centre of the head of the colony. Faecal pellets are throughout the colony.

In life the colour of the sand crowded in the stalk affects its colour. The gelatinous test of the head is darkly pigmented, the colour becoming progressively more intense toward the top of the colony. Around the lower half of the head, the embedded sandy core projecting up from the stalk is closer to the surface and the colour less intense. The colour on the top of the heads is 'blackish-slate' (Ridgeway 1886). Kott (1957a) recorded specimens from Rottnest I. as blackish-green.

In freshly preserved material are both black and tan spherical pigments cells up to 0.04mm in diameter in a layer beneath the surface of the colony, and in the thoracic body wall of zooids. Zooids are otherwise whitish-yellow with a greenish-yellow stomach. In long-preserved colonies from Western Australia the tan colour persists, but not the black.

INTERNAL STRUCTURE: Zooids are relatively long and slender when relaxed, extending from the surface of the head down into the base of the stalk. However, they contract to about 2.5mm. The atrial siphon is longer than the branchial siphon, and is located well down the thorax. There are 3 rows of branchial tentacles. About 15 longitudinal thoracic muscles continue in a wide band along each side of the ventral line of the abdomen, causing it to curl up when contracted. An unperforated prestigmatal area is in the anterior part of the pharynx. The stigmata, perhaps 15 to 20 per row, are difficult to count. The gut and gonads are in the usual position in the posterior end of the abdomen.

A single large embryo is in the atrial cavity of specimens taken from Rottnest I. in March, and Margaret River in January. The larval trunk is 1.7mm long. It is the largest known for an *Eudistoma* species. The tails winds almost three quarters of the way around the trunk. Wide, rather flat median ampullae alternate with the large adhesive organs in the vertical mid-line anteriorly.

REMARKS. Superficially colonies from Western Australia with their crowded zooids in stalked heads resemble those of *E. elongatum*, except they are a darker colour, do not become long and cylindrical, have sand embedded in the stalk and the centre of the head, and have large spherical pigment cells. The pigment cells resemble some found in *E. maculosum* n.sp. and *E. tigrum* n.sp. but are larger. *Eudistoma muscosum* nom. nov.

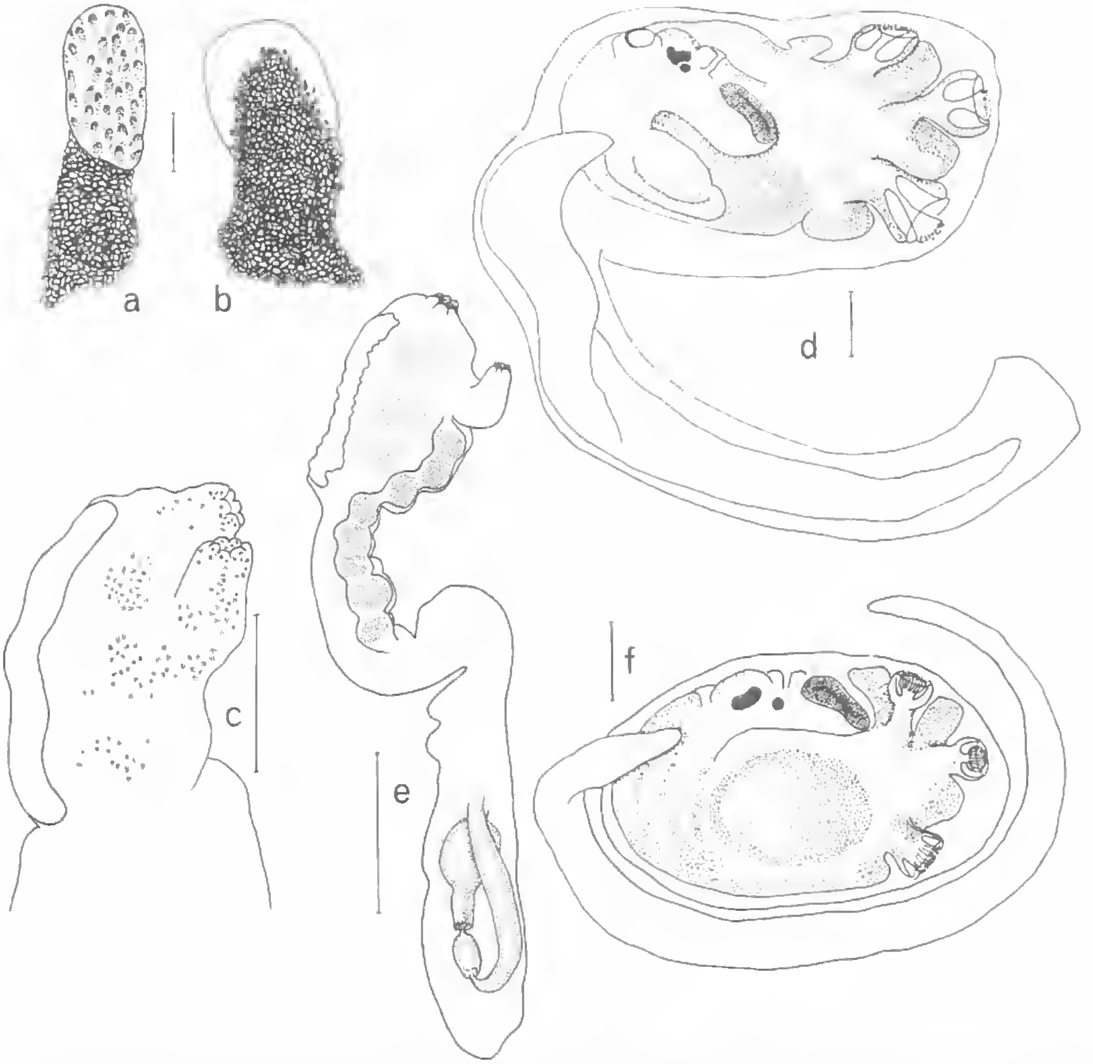


FIG. 79, *Eudistoma globosum*: **a**, colony (QM GH4563); **b**, section through colony showing sand (WAM 815.83); **c**, thorax showing brown pigment in body wall (QM G4579); **d**, larva (QM GH2128). *Eudistoma gracilum* n.sp.: **e**, zooid (holotype QM GH4531); **f**, larva (QM GH4533). Scales: **a,b**, 1cm; **c,e**, 0.5mm; **d**, 0.2mm; **f**, 0.1mm.

has shiny brownish red pigment cells of a similar size in freshly preserved material but they disappear in preservative, and are never black as in the present species. The species are further distinguished by the shape of the colonies and the arrangement of the zooids.

Eudistoma gracilum n.sp.
(Fig. 79e,f)

DISTRIBUTION

TYPE LOCALITY Queensland, Heron I. north reef, coll. P. Kott 15.1.83, holotype QM GH4531; paratype QM GH4532.

FURTHER RECORDS: Queensland (Heron I., QM GH4533 GH4837).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies form smooth-surfaced sheets, up to 6cm in maximum diameter and only about 0.5cm thick. In life, the test is a soft, red or 'orpiment orange' (Ridgeway 1886) translucent jelly resembling a water-ice. Zooids, white or orange, are easily seen through it. Some faecal pellets are in the test. In preservative colonies are a rather dirty, transparent, beige and zooids are green, the green being especially concentrated in the muscles. The soft, sometimes almost mucus-like test fills concavities in the surface of the coralline rubble over which it grows and zooids often are drawn down into these concavities. The substrate thus forms a framework for support and protection of these delicate colonies.

Systems were not identified in the soft test, although it is possible they were present in the living colony, as the atrial siphons are relatively long and probably open in the centre of a circular system. Spherical brown cells, about 0.01mm diameter, are scattered evenly in the test and sometimes these collect together in almost spherical reservoirs in the test.

INTERNAL STRUCTURE: The delicate, relatively small, slightly contracted zooids are only about 2mm long. The 12 longitudinal muscle bands on the thorax, continue along the abdomen in two wide bands. No circular muscles were detected on the thorax. There are only about 10 stigmata per row. The oesophageal neck is long and narrow. The small, smooth stomach and small oval posterior stomach are in the posterior end of the abdomen.

A single embryo is in the atrial cavity of specimens collected in May (QM GH4533). The larval trunk is 0.6mm long and single ectodermal ampullae alternate with the adhesive organs in the anterior mid-line. The tail winds almost three quarters of the way around the trunk.

REMARKS: The species is distinguished by its small zooids with relatively few stigmata, fine and exclusively longitudinal musculature, and the soft test and thin colonies. The larval trunk is about the same length as that of *E. incubitum* n.sp., but is not so deep and its ampullae are not so wide. The larvae of *E. laysani* and *E. elongatum* also are similar, but smaller.

Eudistoma incubitum n.sp.
(Fig. 80)

DISTRIBUTION

TYPE LOCALITY: Queensland (Capricorn Group, NW Wistari Reef, rubble fauna, LWM, coll. P. Kott 11.11.85, holotype QM GH4537, paratypes QM GH4538).

FURTHER RECORDS Queensland (Capricorn Group, QM G11953 GH2268 GH4534 6 GH4565 6 GH4584).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of upright, cylindrical to mushroom-like lobes up to 2cm high. In young colonies (QM GH2268) zooids open on the upper free end of the lobe, and the anterior part of each zooid projects from the surface. Larger lobes have circular to oval heads up to 2cm in diameter, supported by firm cylindrical basal stalks. Sometimes the stalks branch, and numbers of lobes arise from common basal test. Living colonies are white, with transparent test and white zooids, and are the same in preservative. Faecal pellets are in the test, especially in the stalk, but sand is not. Circular systems of 4 or 5 zooids are seen through the transparent test of the head.

The surface test contains evenly spaced, conspicuous spherical cells about 0.05mm in diameter and about 0.3mm apart. These give the colony a speckled appearance when magnified.

INTERNAL STRUCTURE: Zooids are small, about 3mm when strongly contracted. When relaxed they occupy the whole height of the colony and are slender. About 10 longitudinal muscles are on the thorax, continuing along the whole length of the abdomen in up to 7 bands of unequal width on each side, although sometimes only a single wide band is on each side of the ventral mid-line. Contraction of the longitudinal muscles not only makes the oesophagus minutely wrinkled, and the rectum folded and bent, but also bends the abdomen up against the ventral border of the thorax. A band of about 12 circular muscles is around the middle of the thorax. About 10 stigmata are in the anterior row, but they could not be accurately counted in these contracted specimens.

The gut is characteristic of the genus with a small smooth stomach, long duodenal region and oval posterior stomach. Long tubules of the gastro-intestinal gland lie along the proximal part of the rectum. Gonads are in the distal part of the gut loop. The male follicles are relatively large when mature. The proximal part of the vas deferens expands into a long spindle-shaped seminal vesicle when filled with sperm.

In specimens collected in May, July, August and November (QM GH4538 GH4584 GH4565 GH4537 respectively) a row of up to 4 embryos is in the distal part of the oviduct, just posterior to the thorax. Embryos lie in a developmental sequence with the most advanced at the top. They are incubating in the oviduct, and consequently were fertilised there, rather than in the atrial cavity.

Larvae are almost spherical, the trunk about 0.6mm long. The tail is moderately long, reaching about three-quarters of the way around the trunk. The surface of the larval test has the same speckled appearance as the surface test of the adult colony. This is due to terminal expansions of thread-like extensions from the larval ectoderm. These vesicles can be removed with the larval test. They resemble similar structures in the angolanum group of *Eudistoma* (see above: *Eudistoma*; and **larvae** in

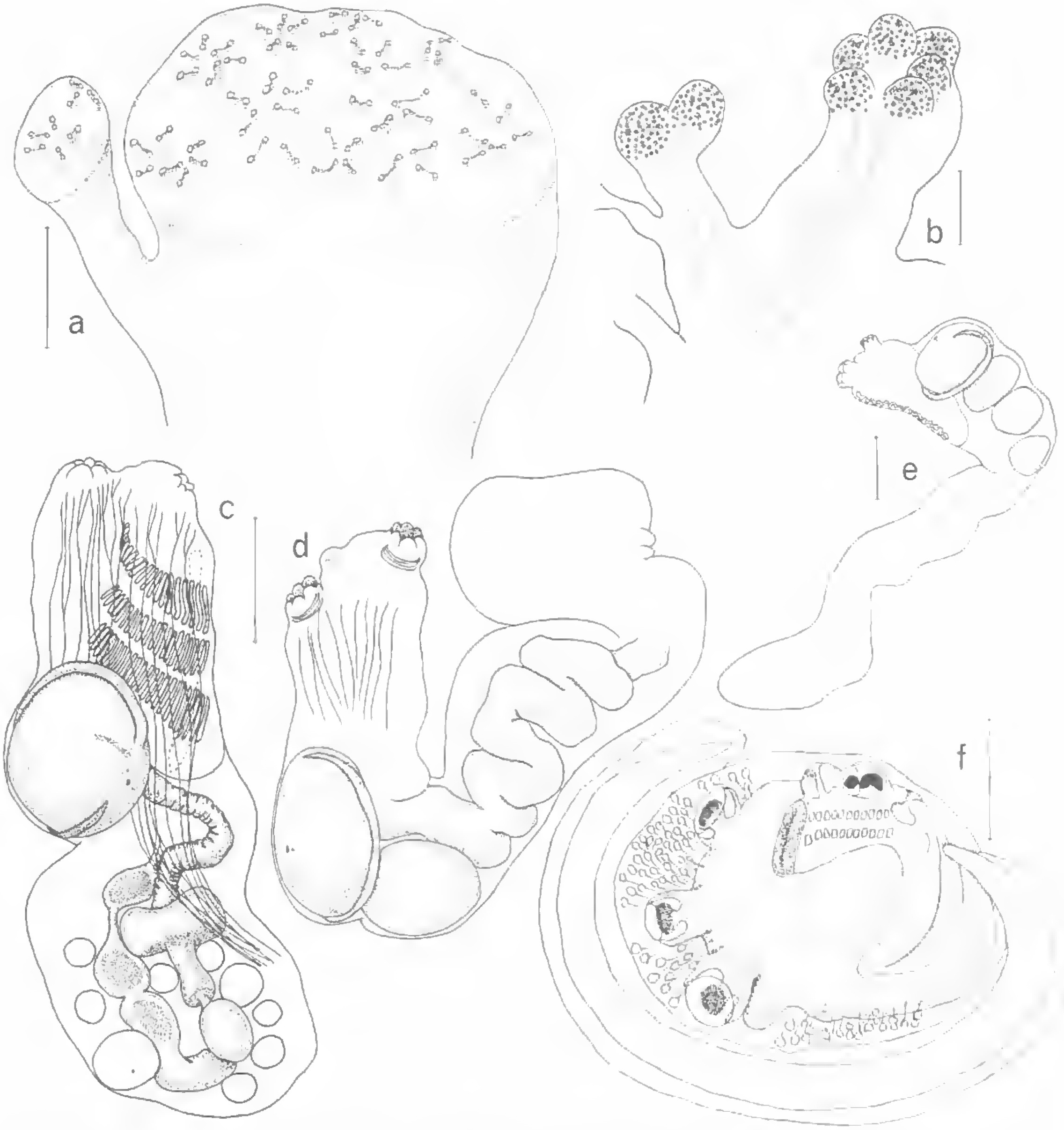


FIG. 80, *Eudistoma incubitum*: **a**, colony showing systems of zooids (holotype QM GH4537); **b**, colony showing speckled test (QM GH2268); **c**, zooid showing body organs (QM GH4584); **d,e** zooids showing incubating embryos (holotype GH4537); **f**, larva (QM GH4584). Scales: **a**, 5mm; **b**, 2mm; **c–e**, 0.5mm; **f**, 0.2mm.

the Annotated Glossary). Paired lateral ectodermal ampullae alternate with the adhesive organs which are almost sessile, on short, wide stalks.

REMARKS: The speckled appearance of both larval and adult test in this species is unique. The presence of developing embryos in the top of the oviduct is also unusual, for in other species examined in the course of this study maturing embryos are in the atrial cavity where fertilisation probably occurs. The spherical shape of the larval trunk is also distinctive. The white transparent, lobed colonies and small zooids sometimes projecting from the upper surface of each lobe resemble small lobes of *E. laysani*. However, in the latter species the living colonies are an iridescent blue and the larvae are smaller with a relatively long, narrow trunk.

Eudistoma laysani (Sluiter, 1900)

(Fig. 81)

Distoma laysani Sluiter 1900, p. 9.
Polycitor laysani: Sluiter 1909, p. 4.
Eudistoma laysani: Millar 1975, p. 221. **Not** Tokioka 1967a, p. 119; 1967b, p. 394.
Distoma parva Sluiter, 1900, p. 6.
Eudistoma parvum: Kott 1957a, p. 77
? *Polycitor regularis* Sluiter 1909, p.
Polycitor (*Eudistoma*) *olivaceum*: Tokioka, 1942, p. 497.
? *Eudistoma album* F. Monniot, 1988, p. 210.

DISTRIBUTION

NEW RECORDS. New South Wales (Botany Bay, AM2206). Queensland (Currumbin, QM GH4539; Burleigh Heads, QM G9268 GH4541; Caloundra, QM GH4546; Mooloolabah, QM GH4545; Noosa, QM GH4543 GH4547; Tannum Sands, QM GH1499; Heron I., QM G10039 G11953 GH2267-8 GH4548-9; Sarina, QM GH4544). Lord Howe I. (QM GH4542).

PREVIOUSLY RECORDED: New South Wales (Lake Macquarie — Kott 1957a). Palau Is (Tokioka 1942). Indonesia (Sluiter 1909, Millar 1975). Phillipines (Millar 1975). Hawaii (Laysan — Sluiter 1900).

This is a common and conspicuous species in the western Pacific, and is found higher up the intertidal region than any other aplousobranch ascidian. The majority of the records are from the intertidal region, sometimes even at mid-tide level. Only the record from the Phillipines (Millar 1975) is from a greater depth (22m).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of a basal mass of common test supporting numerous lobes. Each lobe consists of a cylindrical, sometimes branched stalk, and a slightly expanded head, its upper surface flat, rounded, or conical. Lobes are about 3mm to 1cm high. Stalks are firmer than heads, which have delicate transparent test. Abdomina of the zooids are crowded, parallel to one another down the length of the stalk and into the basal test. In addition to the abdominal portions of the zooids, the stalks contain faecal pellets, and both confer their colour to the stalk and make it quite opaque. Epizooites and other foreign particles are often on the stalk and basal test but never any embedded sand.

Atrial apertures are always anterior to, or more central than the branchial apertures, but there are no systems. In small, juvenile lobes with up to 6 zooids the anterior ends of the zooids project separately above the surface of the head, but in larger colonies only the apertures protrude. Larger lobes with rounded, club-shaped or pointed heads contain up to 100 zooids opening all over the surface of the head. In many specimens the size of the lobes from one basal mass is varied, and small, presumably developing lobes, such as those described by various authors for *E. laysani*, are present.

The separate lobes of living colonies when inflated appear confluent with one another. They are white with 'pale antwerp blue' (Ridgeway 1886) iridescence. In preservative the blue pigment only occasionally persists and the colonies are pink or white.

INTERNAL STRUCTURE: Extended zooids are often particularly long, with a long, narrow oesophageal neck. However, the thoraces are seldom more than 1mm. Contracted zooids are no more than 2mm long. Zooids are narrow and much less robust than most other species of this genus. Both branchial and atrial lobes are large and triangular, and a distinct circular muscle surrounds each relatively short siphon. From 8 to 16 fine longitudinal muscles are on the thorax. These extend along each side of the abdomen as separate fine muscles rather than wide bands. Circular muscles, beneath the longitudinal bands, are also fine and are confined to the middle of the thorax. There are 16 long tentacles in a posterior row and further tentacles in 3 additional anterior rows. The atrial siphon originates opposite the first row of stigmata, well down the dorsal surface. A long prestigmatal region is in the anterior part of the pharynx.

The stigmata can be more easily counted in this than in other species of this genus, possibly because of the relatively fine musculature. Only 12 stigmata are in the posterior row, but up to 20 are in the anterior row. The dorsal 3 stigmata in the anterior row curve up along the mid-line, toward the dorsal ganglion. The usual small, smooth-walled stomach is at the posterior end of the abdomen. There is an oval posterior stomach but it is not always distinct. Tubules of the gastro-intestinal gland extend anteriorly along the ascending limb of the gut loop.

Mature gonads and up to 8 embryos are in the atrial cavity of specimens from Heron I. collected in February (QM GH4550). Specimens from Batehaven collected in April (MV F53397), from Botany Bay collected in May (QM GH4540), and from Caloundra (QM GH4546) and Noosa Heads (QM GH4543) collected in November, have a similar number of embryos in the atrial cavity.

Larvae are small, the trunk only 0.4 to 0.5mm long. The tail is wound halfway around it. There is an otolith and an ocellus, and 4 single median ectodermal ampullae alternate with the stalked adhesive organs.

REMARKS: The multilobed colonies, with delicate transparent test on the terminal part of the lobes, and without embedded sand; small

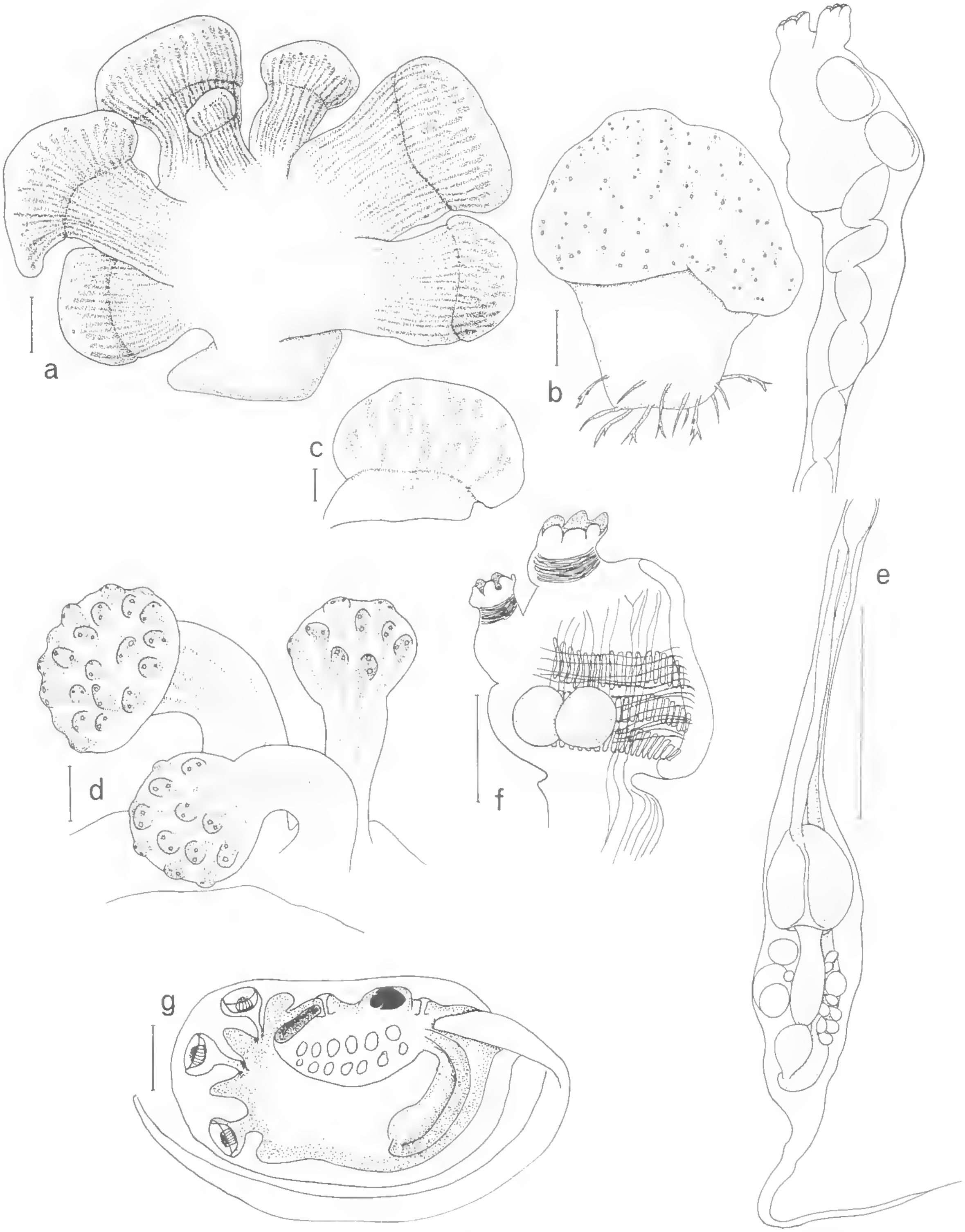


FIG. 81, *Eudistoma laysani*: **a**, large colony (QM GH4541); **b–d**, smaller colonies (QM GH1499 GH4548 AM Y2206); **e**, zooid, with 4mm of oesophageal neck excised (AM Y2206); **f**, thorax with incubating embryos (AM Y2206); **g**, larva (QM G9268). Scales: **a**, 2mm; **b–e**, 1mm; **f**, 0.5mm; **g**, 0.1mm.

zooids with fine muscles; and small larvae are all characteristic of the species, as is their whitish-blue iridescence. Their colour resembles that of *Ritterella prolifera* (Oka, 1933), but in the latter species the lobes are sessile rather than stalked (see Kott 1972d).

A wide range exists in the shape and size of the lobes of these colonies, occasionally within the one colony (QM GH4540 GH4550). More often the stalked lobes are a uniform size in each colony. Variations in their diameter are probably the result of growth. However, smaller lobes occur more frequently in the tropics than in temperate waters, and there may be a cline in the populations. The colonies resemble lobes of *E. elongatum* in the absence of systems, blue iridesence and small larvae, and it is possible that the latter species is conspecific, representing populations with long, rope-like heads at one end of a cline.

The type material of *Eudistoma laysani* (Sluiter, 1900) from Laysan has small lobes, each with a single circle of zooids with their anterior ends projecting from the free end of the lobes. Millar (1975) recorded similar specimens from the Philippines and Indonesia. Millar's specimens contained small larvae similar to those in the newly recorded material. The zooids in the lobes of the Australian material usually are more numerous, crowded and not arranged in circles, but single circles do occur in the smaller lobes. Thus, until some character is identified to indicate different species, the specimens referred to in the synonymy and distribution (above) are regarded as conspecific.

Tokioka's (1967a,b) specimens from the Palau Is and from Vietnam, respectively, with long, rather irregular colony lobes and relatively large larvae are not of this species. The colonies from Vietnam (Tokioka 1967b) resemble those of *Eudistoma toealensis* Millar, 1975, and the larvae also are similar. Larvae of the Palau Is specimen (Tokioka 1967a) suggest it is yet another species.

Eudistoma segmentatum (Sluiter, 1909) has a similar colony but a larger zooid than *E. laysani*. *Eudistoma parvum* (Sluiter, 1900) recorded from Laysan, and a possible synonym from Japan *E. parvum* Oka, 1927d (see also Tokioka 1953, 1954b), is another similar species, although the Japanese colonies are solitary stalked heads rather than the multi-lobed ones of the present species.

Zooids (but not the colonies) of the present species resemble those of *Eudistoma gracilum* n.sp. in their small size and fine muscle bands. The colonies of the latter species are flat sheets rather than separate stalked lobes joined to a basal test mass or stolon, and the test is extremely soft and mucus-like.

Eudistoma maculosum n.sp.

(Fig. 82, Plate 16a–d)

Eudistoma renieri: Kott, 1957a, p. 74; 1972a, p. 10, 1972b, p. 171.

Eudistoma pyriforme: Kott 1972a, p. 9; 1976, p. 58 (part, specimen from Mallacoota Inlet).

DISTRIBUTION

TYPE LOCALITY. South Australia (Ward I., 20–25m, coll. N. Holmes and S. Shepherd 31.3.82, holotype QM GH1304; Topgallant I., 5m, coll. N. Holmes and S. Shepherd 29.3.82, paratypes QM GH1278; Flinders I., Investigator Group, 8m in caves, coll. N. Holmes 10.4.83, photo index PE 0024 R965/R967, paratypes QM GH2391).

FURTHER RECORDS: Western Australia (Pt. Peron, AM Y1299 Kott 1957a). South Australia (Great Australian Bight — Kott 1972a,b; Ward I., QM GH1282). Victoria (Mallacoota Inlet – MV F5482 Kott 1976). New South Wales (Jervis Bay, QM GH4605).

DESCRIPTION

Colonies form firm, fleshy, flat-topped oval cushions to extensive fleshy sheets 0.5 to 1.5cm thick, with rounded borders. They are fixed by the whole or part of the basal test. The surface is smooth. Zooids are in circular systems of 6 to 8. Living colonies are white with black zooids. In preservative all colonies are opaque, slate-grey to black with blackish to blue zooids and brown to tan pigment cells concentrated in patches near the surface of the otherwise whitish, cloudy, translucent test. These brown to tan pigment cells form an inconspicuous, mottled, rusty-looking pattern on the surface of the colony. South Australian specimens are white with black zooids, and the specimen from NSW is brown and white.

Sand is embedded in the middle layer of test and becomes less crowded toward the base. Sand is usually absent from the upper half of the colony.

INTERNAL STRUCTURE: Zooids are robust with about 20 longitudinal muscles on the thorax that continue onto the abdomen in a wide band on each side of the mid-ventral line when contracted. In relaxed zooids the longitudinal muscle bands are separate from one another. There is an almost continuous coat of circular thoracic muscles. Circular muscles are on the siphons, but they do not form a distinct sphincter. About 20 long stigmata are in each row. The gut has the divisions characteristic of *Eudistoma*.

A single large embryo projects from the atrial cavity in colonies collected from Point Peron (WA) in January (AM Y1299), from South Australia in November (see Kott 1972a) and from

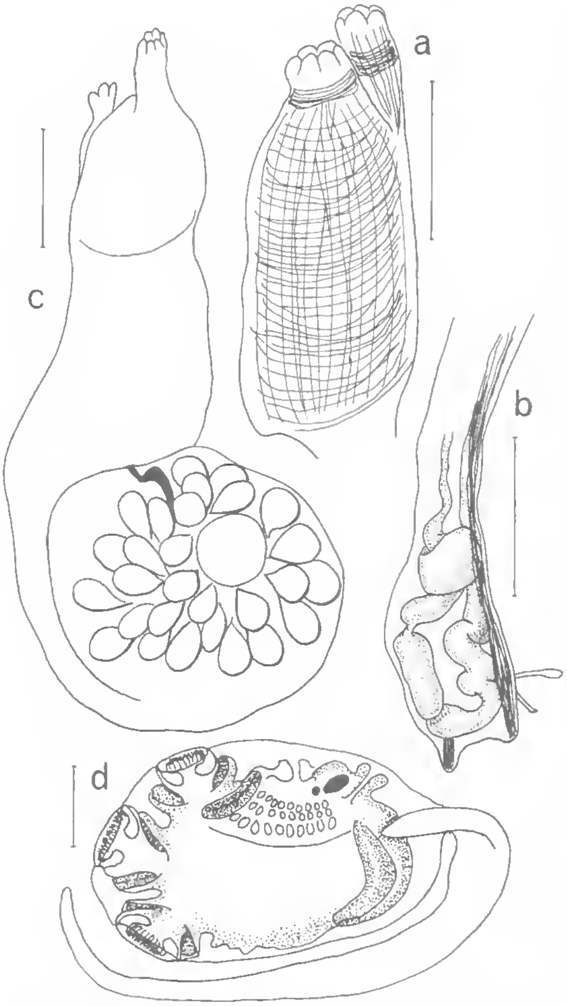


FIG. 82, *Eudistoma maculosum* n.sp.: **a**, thorax showing muscles (holotype QM GH1304); **b**, abdomen showing gut loop and longitudinal muscles (holotype QM GH1304); **c**, zooid showing lower third of abdomen contracted up against middle third (QM GH4605); **d**, larva (AM Y1299). Scales: **a–c**, 0.5mm; **d**, 0.2mm.

Jervis Bay in August (QM GH4605). The larval trunk is 0.9mm long and the tail is wound almost three-quarters of the way around it. Larvae are unusual in having 3 large adhesive organs each with a short stalk and large, vertically elongated, oval platform of columnar cells in a shallow epidermal saucer. Bract-like epidermal ampullae are in the mid-line, one dorsal and one ventral to the base of each of the adhesive organs. Larvae have 3 rows of stigmata.

REMARKS: This commonly encountered, robust temperate species resembles, and may be related to, the tropical species *Eudistoma tigrum* n.sp. Both have the same pattern of surface pigmentation which, in preserved material appears as rust-like patches. They also form extensive rather sheet-like colonies with rounded borders, and have their zooids in circular systems. The principle distinctions between them are in the larvae — the present species having a larger larva with bract-like ectodermal ampullae and vertically elongated platforms of adhesive cells in the short, thick-stalked adhesive organs, while those of *E. tigrum* n.sp. are smaller, have adhesive organs with long narrow stalks alternating with median paired ampullae. Where larvae are not available, the temperate — as opposed to tropical — range of the present species must be relied on to separate it from *E. tigrum* n.sp. Larvae with the same elongate adhesive organs are known for *E. glaucum*, *E. purpureum* n.sp. and *E. marianense* Tokioka, 1967a, but the larval trunk in these species is much longer (1.2mm, 1.5mm and 1.5mm respectively), and their colonies are mushroom-like with short thick stalks (*E. glaucum* and *E. marianense*), or large rounded, sessile cushions (*E. purpureum*), rather than the extensive sheets of the present species. *Eudistoma muscosum* nom. nov. has larvae of similar length and the same elongate adhesive organs as the present species. The test is also darkly pigmented with tan and dark coloured pigment cells. However, the two-toned colour pattern of *E. maculosum* is not present, and the colonies do not form the same extensive sheets.

In one specimen (Kott 1972a, Wright I.) the second and third adhesive organs are joined, and there is one long protruding ridge of columnar cells.

Eudistoma malum n.sp.

(Fig. 83a,b)

DISTRIBUTION

TYPE LOCALITY. Queensland (Capricorn Group, Heron I., side of bommie 10m, coll. N. Coleman 20.7.73, AMPI 87, holotype QM G11939; Heron I., 8 10m, coll. P. Kott March 1975, paratype QM G11940).

FURTHER RECORDS. Queensland (Capricorn Group, QM GH4635 9 ?GH4851; off Gordonvale, QM GH798).

DESCRIPTION

EXTERNAL APPEARANCE: Smaller colonies consist of top- to mushroom-shaped lobes, often with an almost completely spherical head, about 2 to 3cm diameter, on a short, thick stalk. The largest colony available (QM GH798) is an upright cone 4cm high and 3cm diameter. Sand is in varying concentrations in the stalk and sometimes extends up into the centre of the head. Zooids open all around the head, and are in circular systems of 3 or 4 zooids. In life the holotype colony was reported a 'yellow ball ascidian'. However, the paratype and other colonies are shades of purple 'burnt sienna' at the top of the stalk to 'madder brown' on top; 'cinnamon rufus' shading to a transparent stalk (Ridgeway 1886); and maroon purple with a sandy stalk. In preservative colonies become translucent and greyish white with some minute (0.01mm) bluish-black to brown pigment cells in the surface layer, and fairly evenly distributed through the remainder of the test. These cells are also found lying free in the space between the zooid and the test. Often a white suspension is in the surface test. Usually pools of greenish-brown to brown pigment cells are at the base of the stalk. Sand embedded in the stalk affects its colour. In preservative zooids are cream to pink.

INTERNAL STRUCTURE: Zooids are robust but relatively short, about 3mm long when contracted. The atrial siphon usually is 2 to 3 times the length of the branchial siphon. About 15 longitudinal thoracic muscles continue along the side of the abdomen. On the thorax, these muscles tend to form a rather regular meshwork with the internal circular muscles. Moderately conspicuous sphincters are around the siphons. There are about 16 stigmata per row. The abdomen is of the usual form with gonads in the gut loop. The testis follicles sometimes form a fairly compact, almost spherical mass of follicles at the side of the distal end of the gut loop, but sometimes are loosely disposed in the gut loop.

Up to 4 developing embryos are lined up, overlapping one another in the peribranchial cavity. Larvae, which are in both holotype and paratype colonies, have an elongate trunk 0.75mm long with relatively long tail wound about two-thirds the way around it. A row of 4 rounded lateral ampullae is along each side of the median adhesive organs at the anterior end of the trunk. The ventral pair are flattened plates on a long base.

REMARKS: The larva of this species, with its long trunk, and narrow plate-like ventral ectodermal ampullae, is distinctive. However the adults, especially after preservation, have few distinguishing characters except the evenly distributed spherical pigment cells and upright colonies.

Eudistoma glaucum has similar stalked heads and zooids, although the present species lacks its green pigment. *Eudistoma globosum* has a similar colony but lacks the circular systems. The larval trunk of *E. tigrum* n.sp. is the same size as the present species, but its colonies are flat sheets rather than upright lobes and it has a distinctive colour pattern in the surface test. Preserved colonies of the present species have a white suspension in the surface, and accordingly it can be confused with *E. anaematum* n.sp. which is distinguished by its low cushion-like colonies without stalks, smaller pigment cells, and longer atrial siphons. *Eudistoma muscosum* nom. nov. has a similar compact spherical mass of testis follicles, but it has more crowded and larger pigment cells, lacks both the stalk and white surface suspension characteristic of the present species, and its preserved zooids are more intensely coloured, being reddish-brown rather than pink to cream. One long-preserved specimen, possibly this species, from Heron I. (QM GH4851) has lost all colour except for a wide collar of spherical orange vesicles around the duodenum.

Eudistoma microlarvum n.sp.

(Fig. 83c,d)

DISTRIBUTION

TYPE LOCALITY: Queensland (North Stradbroke I., Point Lookout, near low tide mark, coll. A. Rozefelds 17.11.78, holotype QM GH4520; paratypes QM GH4521).

FURTHER RECORDS: Queensland (Hervey Bay, QM GH938).

The species has so far been recorded only in sandy habitats, from a small part of the southern Queensland coast.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are flat investing sheets or cushions, up to 1.5cm high, and sometimes with the naked upper surface divided into irregular lobes. The test is almost transparent and although it has sand grains embedded, the sand is relatively sparse in the lower half of the colony and sometimes absent from the upper half around the thoraces of the zooids.

The small zooids, which are 4mm long when extended, are white and thread-like in preservative, and can be seen extending vertically through the transparent test. They do not form systems. The separately opening atrial and branchial apertures can be demonstrated by washing a drop of stain across the surface of the colony.

INTERNAL STRUCTURE: Both the branchial and atrial siphon are relatively short, each with a short sphincter. Thoracic muscles are fine, about 12 longitudinal bands and only about 14 transverse ones. Longitudinal muscles extend along each side of the ventral half of the abdomen well separated from one another. They are not gathered into a continuous wide band. There are only about 8 stigmata per row. The oesophageal neck is long and narrow, and the small, smooth-walled

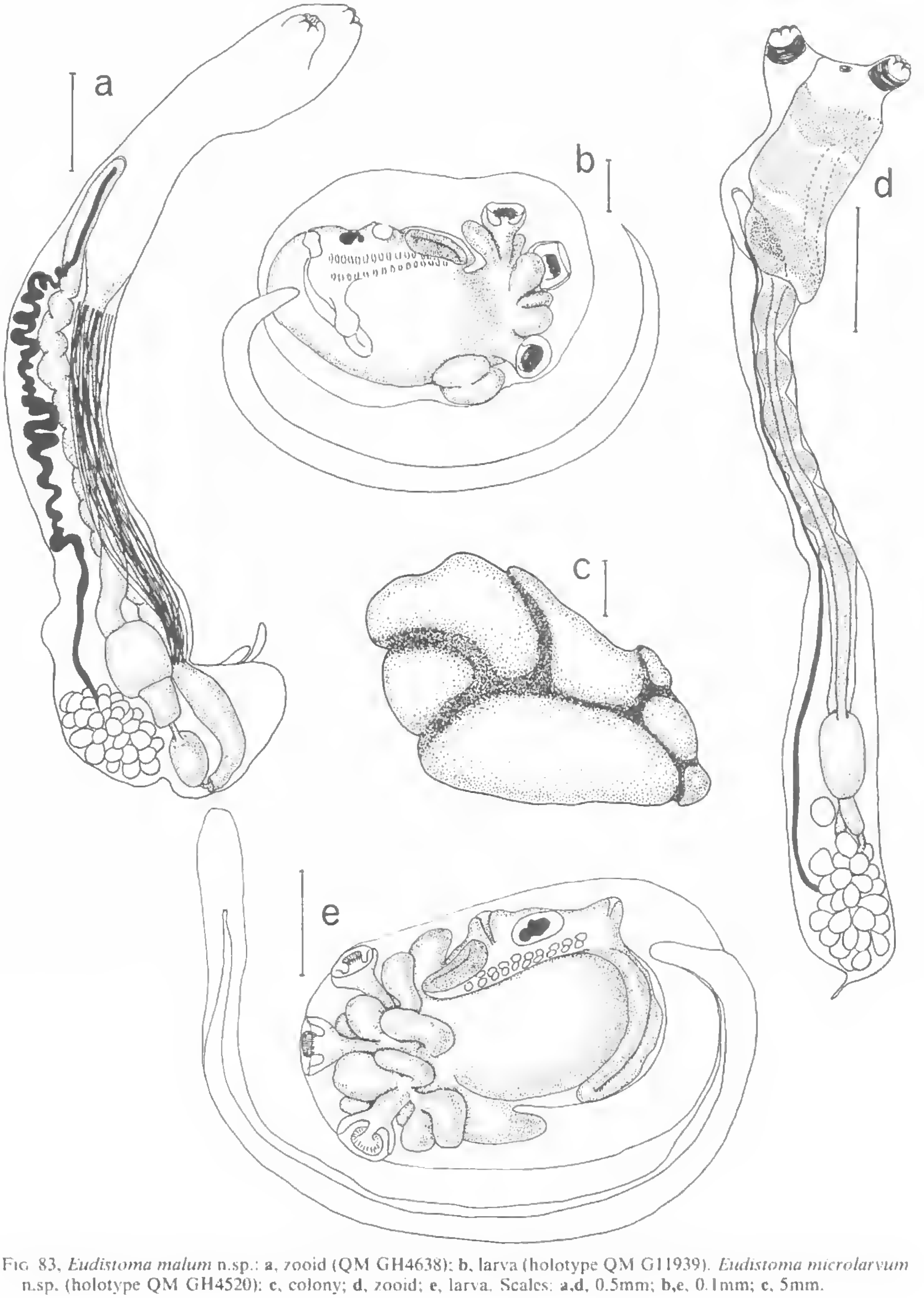


FIG. 83, *Eudistoma malum* n.sp.: **a**, zooid (QM GH4638); **b**, larva (holotype QM G11939). *Eudistoma microlarvum* n.sp. (holotype QM GH4520): **c**, colony; **d**, zooid; **e**, larva. Scales: **a**,**d**, 0.5mm; **b**,**e**, 0.1mm; **c**, 5mm.

stomach is in the posterior end of the abdomen. The duodenal area is long and tapers to a small, oval, posterior stomach at the posterior end of the descending limb of the gut loop.

A long, grape-like cluster of male follicles at the left side of the gut loop slightly overlaps the pole of the gut loop. The type material, has a single embryo in the atrial cavity, mature male follicles and the vas deferens filled with sperm and expanded into a long spindle-shaped seminal vesicle at its proximal end.

The larva is small with a trunk about 0.4mm long. It has lateral as well as median ampullae, an ocellus and otolith.

REMARKS. Colonies of this species are readily distinguished from *Eudistoma constrictum* (which also is sandy, investing and lacks systems) by its small thread-like zooids.

Eudistoma museosum nom. nov.
(Fig. 84)

Polycitor mollis Sluiter, 1909, p. 11.
Not *Distoma molle* Ritter, 1900, p. 605. – *Eudistoma molle*: Van Name 1945, p. 128.

DISTRIBUTION

NEW RECORDS. Queensland (Capricorn Group, QM G11941 G11944–7 GH1349 GH4568–78; Lizard I., QM GH4592 AM Y2207).

PREVIOUSLY RECORDED. Indonesia (ZMA TU.801 Sluiter 1909).

DESCRIPTION

EXTERNAL APPEARANCE. Most colonies are smooth, shiny and round to lozenge-shaped or irregular pillows about one to 2cm in maximum extent and up to 0.5cm high. They are fixed by most of the basal surface. The colony from Lizard I. (AM Y2207) is larger. It is an upright lobe at least 5cm high and 4cm in diameter. In life colonies occur in a variety of colours in the range khaki, olive to brown (Ridgeway 1886: 'tawny-olive', 'sepia', 'wood-brown', 'mustard-green', 'clove-brown', 'olive', 'olive-green', 'bay', 'bistre'). Occasionally the colour shades from brown at one end to tawny olive at the other. In preservative the colour becomes black-brown or brown, and later a cloudy greenish-grey. In freshly preserved material a mass of opaque tan-coloured pigment cells (0.04mm in diameter) pack in the test at thoracic to oesophageal level, below the surface of the colony. Also minute (0.02 to 0.03mm) shiny reddish spheres are scattered in the test. The preservative stains reddish to brownish-yellow. In freshly preserved material zooids are black, although this persists only in the anterior part of the thorax. Zooids, especially in the endostyle, gut and gonads, usually become the reddish-brown colour of the preservative. The test is relatively transparent in preservative and is soft. Sand and faecal pellets embed in the test in the base of the colony. Zooids are in circular systems of about 5, with their atrial apertures near one another in the centre of the circle.

INTERNAL STRUCTURE. Zooids are large (up to 5mm long even when contracted) and robust. The oesophageal neck is relatively thick. The atrial siphon is 2 to 4 times longer than the branchial siphon, and both are relatively wide. Strong circular muscles surround each siphon fairly evenly along their length. There are about 20 strong thoracic longitudinal muscle bands and more numerous circular ones. Longitudinal bands continue along each side of the abdomen separately and are not gathered into a band. They terminate just posterior to the stomach on each side of the mid-ventral line. Thus, when contracted the oesophageal neck is shortened, the oesophagus and rectum are horizontally wrinkled and pleated, but the posterior end of the gut loop is not much affected. About 25 stigmata are in the anterior row and only 18 in the posterior row. The dorsal part of the anterior row of stigmata curves forward along each side of the dorsal mid-line.

A long duodenal area and a distinct oval posterior stomach lie in the posterior part of the descending limb of the gut loop. Long tubules of the gastro-intestinal gland curve around part of the rectum opposite the duodenum. In specimens collected in November the testis follicles are mature and form a large, compact spherical mass on the left side of the posterior end of the gut loop. The vas deferens is conspicuous with a long, spindle-shaped expansion packed with sperm as it extends anteriorly dorsal to the rectum.

One or 2 embryos are in the atrial cavity of specimens collected in August (QM GH1349) and January (QM GH4568). The larval trunk is almost spherical, and about 1mm long. The 3 adhesive organs are of different sizes. Each has a wide, slightly elongated platform of adhesive cells, surrounded by a shallow ectodermal cup. The tail is wound about three-quarters of the way around the trunk. The larval epidermis contains dark pigment concentrated in the 2 posteriorly projecting horns of the larval haemocoel — one each side of the base of the tail. These larvae have 3 rows of stigmata.

REMARKS. Living specimens are distinguished by their brown khaki-olive green colour, but in preservative by the soft translucent test, minute, shiny, spherical (red in preservative) and opaque tan pigment cells, the large compact spherical mass

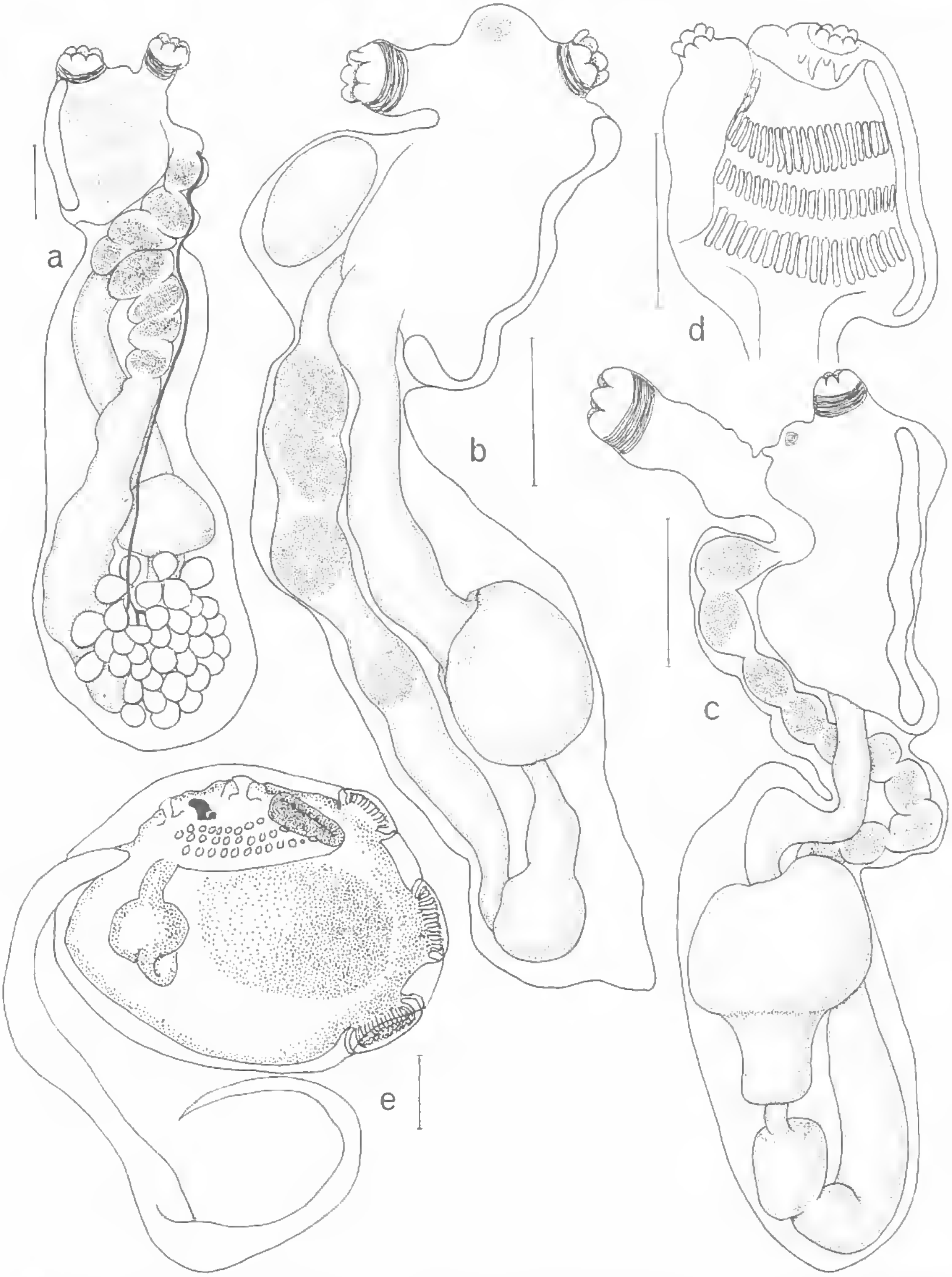


FIG. 84, *Eudistoma muscosum* nom. nov.: **a–c**, zooids showing various positions of the atrial siphon (QM GH457 GH1349 GH4570); **d**, thorax, showing dorsal end of row of stigmata continuing alongside mid-dorsal line (QM GH4568); **e**, larva (QM GH4568). Scales: **a–d**, 0.5mm; **e**, 0.1mm.

of testis follicles and the reddish-brown or black zooids.

The type specimen (ZMA TU.801) is a soft, fleshy, sessile cushion from which most of the colour is now lost leaving the test almost transparent. Some brown pigment remains in the zooids around each of the apertures. Zooids are robust with a large compact mass of male follicles as in the newly recorded material. Although Sluiter recorded fewer stigmata, there are at least 15 in the type specimen, the exact number being difficult to determine owing to the contracted condition of the zooids.

Long-preserved colonies in which the colour has faded altogether can be confused with *Eudistoma purpureum* n.sp. although the latter species has larger larvae. *Eudistoma tigrum* n.sp. also has robust zooids and looses its colour in preservative, but has sheet-like rather than cushion-like colonies, and smaller larvae with flattened leaf-like ampullae and small, narrow-stalked adhesive organs.

The accumulation of dark pigment in the 2 posterior horns of the larval haemocoel is reminiscent of the angolanum group of *Eudistoma*, although these have more ampullae than the larvae of the present species.

Eudistoma ovatum (Herdman, 1886)
(Fig. 85a–f)

Psammaplidium ovatum Herdman, 1886, p. 246.
Eudistoma ovatum: Hastings, 1931, p. 82. Kott, 1972e, p. 43 (part, specimen from St. 773).
Polycitor arenaceus Sluiter, 1909, p. 13.
Polycitor scaber Sluiter, 1909, p. 25.
Eudistoma pyriforme: Tokioka, 1967a, p. 110.
? *Eudistoma vulgare* Monniot, 1988, p. 215.

DISTRIBUTION

NEW RECORDS: Queensland (Hervey Bay, QM G9269 G11938 GH4594; Tannum Sands, QM GH4595–6; Capricorn Group, QM G11968 G11971 GH4598–9 GH4601–4; Yeppoon, QM GH4597; Redbill I., QM GH4600; Lizard I., QM G11970.

PREVIOUSLY RECORDED: Western Australia (Cape Boileau – Hastings 1931). Queensland (Low Is – QM G13510 Hastings 1931). Northern Australia (Torres Strait – Herdman 1886; Gulf of Carpentaria – AM Y1060 Kott 1972e). Indonesia (ZMA TU805 type *E. scaber* Sluiter, 1909). Palau and Gilbert Is (Tokioka 1967a).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are firm encrusting sheets, up to 1cm thick. They grow over irregularities in the substrate so that the surface appears raised into lobes and swellings. Otherwise the surface is even, without projections or depressions. Sand is evenly distributed throughout the otherwise colourless and transparent test, but possibly is less crowded at thoracic than at abdominal level. Faecal pellets are also in the test. Zooids are pink, with a brownish stomach.

Zooids are in circular systems, 2.5mm in diameter with up to 7 zooids per system. Zooid openings are reasonably conspicuous owing to the interruption of the sand where each opens to the surface. They are evenly spaced at the surface but internally abdomina cross one another irregularly.

INTERNAL STRUCTURE: Zooids are relatively small, the contracted thorax being quite narrow and only 1mm long. The atrial siphon is long and muscular. The branchial siphon also is well developed with a wide band of branchial tentacles. Branchial and atrial lobes are rounded. About 12 to 25 thoracic longitudinal muscle bands overlie about 30 transverse ones. Longitudinal muscles continue in two long bands on each side of the abdomen. Often the whole abdomen is folded up against the thorax owing to the strong contraction of the ventral body muscles. There are at least 20 stigmata per row.

Gonads, stomach, and the usual divisions of the gut distal to the stomach, are in the posterior end of the abdomen. They are obscured by the contraction of these small zooids, in which the oesophagus is wrinkled and rectum kinked and twisted along the whole length of the zooid.

Up to 5 embryos are in the atrial cavity of specimens collected in April from central Queensland, in April, May and October from Heron I., and in July from Redbill I. (QM GH4595–9 GH4604 GH4600). Larvae are small, the trunk only 0.6mm long. The tail winds almost three-quarters of the way around the trunk to the left of the adhesive organs. Three slender-stalked adhesive organs are in the median line anteriorly. Dorsal and ventral median ampullae each have a parietal branch on each side. Each of the 2 lateral ampullae on each side also have a parietal branch near the base. Fine projections from the ectoderm around the apertures extend into the larval test.

REMARKS: The other sandy species of *Eudistoma* known from tropical waters in which the zooids are in simple circular systems without actual cloacal cavities are *E. amplum* and *E. pyriforme*. The latter has pyriform colonies that distinguish it from the present species. *Eudistoma amplum* has large zooids and larvae and contains large, spherical symbionts in the test, as well as the sand, and the sand is seldom evenly distributed as it is in the present species.

The sandy temperate species *E. sabulosum*, has thicker colonies than the present species, the

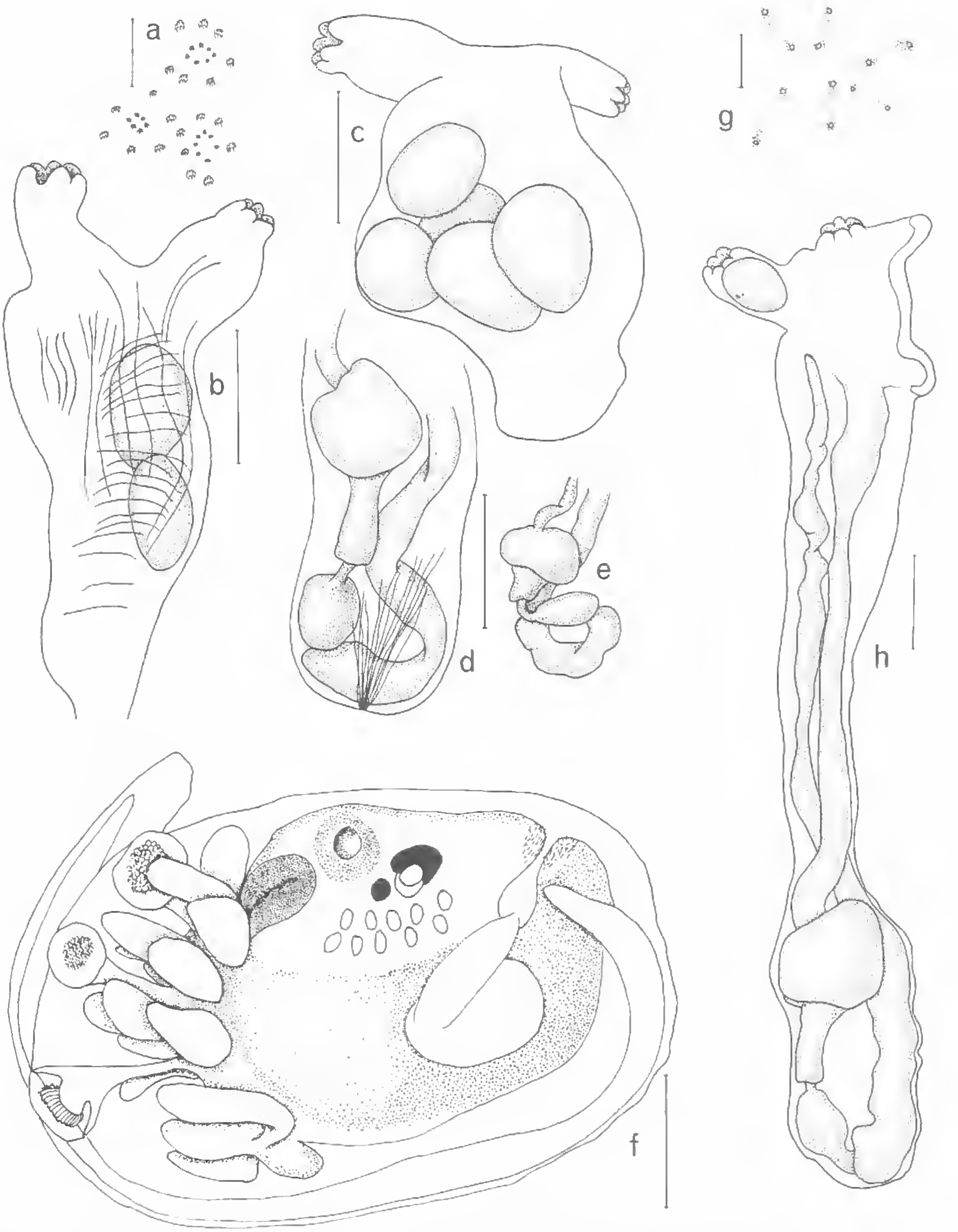


FIG. 85, *Eudistoma ovatum*: **a**, circular systems seen from the surface (QM GH4596); **b,c**, thoraces with incubating embryos (QM GH4604); **d,e**, gut loops from contracted zooids (QM G11969); **f**, larva (QM GH4595). *Eudistoma pratulum* n.sp.: **g** a system of zooids from the surface (paratype QM GH4607); **h**, zooid (holotype QM GH4606). Scales: **a**, 2mm; **b–e,h**, 0.5mm; **f**, 0.1mm; **g**, 1mm.

surface of the colony is not as smooth and the zooids are smaller, with not more than 10 stigmata per row.

Hastings (1931) concluded there were 3 sandy species of *Eudistoma* from Australian waters, *viz. E. ovatum* (Herdman, 1886), *E. angolanum* (Michaelsen, 1914) and *E. pyriforme* (Herdman, 1886). She compared a large (16cm wide and 9cm high) colony from Cape Boileau, north-western Australia (that resembles the newly recorded material) with the type specimens of *E. ovatum* Herdman, 1886) and a smaller specimen from the Great Barrier Reef, and considered all 3 of these specimens to be conspecific. A part of the Great Barrier Reef specimen examined by Hastings is in the Australian Museum (AM Y13510). It appears part of the colony (bisected along the longitudinal axis) figured by Hastings (1931, p. 85, text fig. 8c). In this specimen the test is impregnated with sand, zooids open all along the surface, and although a few abdomina run parallel to the long axis, most lie almost perpendicular to the surface and cross one another. It appears a slice off the surface of a larger colony rather than a portion of a stalked one.

Eudistoma vulgare Monniot, 1988 has similar colony, zooids and larvae to those of the present species and appears a synonym.

Although *Polycitor scaber* Sluiter, 1909 was reported to have only 6 or 7 stigmata per row, reexamination of the single known specimen (ZMA TU805) has shown it to have a similar number to that found in the newly recorded specimens, with an equally wide band of branchial tentacles and the sandy colony characteristic of this species.

The fine ectodermal projections into the larval test around the apertures occur in many *Eudistoma* spp. (see Annotated Glossary: **larvae**).

Eudistoma pratulum n.sp.

(Fig. 85g,h)

Distribution

Type Locality: Queensland (Heron I., rubble fauna, low water mark, coll. P. Kott May 1987, holotype QM GH4606, Heron I., Blue Pools rubble fauna, coll. PK 9.11.85, paratype QM GH4607).

Further Records: None.

Description

External Appearance: Colonies are large (up to 8cm long, 4cm wide and about 1cm thick) firm but fleshy and rather irregular sheets. In life they are creamish or 'sage-green' with 'pea-green' zooids (Ridgeway 1886), slightly translucent and with a slightly rough rather than smooth surface. In preservative the test is brownish-grey, sometimes darker at one end than the other as a result of the crowding of minute dark pigment cells. Zooids are brownish-cream in preservative, the stomach brown and the embryos orange. There are shiny brown pigment cells 0.02 to 0.03mm in the test and lying in the space between the zooid and the test, probably released in blood from severed vessels. Some white suspension, similar to that found in *Eudistoma anaematum* n.sp., is in the surface test, and large pools of dark pigment cells are in the basal test. Zooids are arranged in circles of 5 or 6.

Internal Structure: Zooids are of moderate size, about 5mm long in a fairly relaxed condition. The atrial siphon is often much longer than the branchial siphon. The sphincter muscles around each aperture are narrow and not conspicuous. About 10 to 12 fine longitudinal thoracic muscles continue along each side of the abdomen in several bands. About 25 fine circular muscles are on the thorax. Branchial tentacles are confined to a narrow zone at the base of the branchial siphon, and are in 3 circles. Tentacles are not numerous, about 6 larger ones are in the outer circle, 6 moderate-sized ones in the second circle, and more numerous and irregularly distributed smaller ones in the anterior circle. Stigmata number 25 in the anterior row which curves anteriorly along each side of the mid-dorsal line, but only 18 in the posterior row.

The gut has the usual subdivisions found in this genus. The oval posterior stomach is well defined. Large pyriform testis follicles are tucked into the pole of the gut loop of specimens collected in May (QM GH4606). A single embryo up to 0.75mm long is in the atrial cavity of the zooids of this specimen, although mature larvae were not developed and their structure is not known.

Remarks: Although these colonies are green, sometimes with green zooids, they are not the same opaque shiny green of *Eudistoma glaucum*. The extensive, flat, irregular translucent colonies with a rather rough surface also distinguish them from *E. glaucum* and *E. muscosum* nom. nov. The latter species also has spherical pigment cells about the same diameter as those in the present species. However, the larger, crowded, granular-looking tan cells of *E. muscosum* nom. nov. are not present in *E. pratulum*. Zooid colour in preservative is also different — *E. muscosum* nom. nov. has brownish-red zooids the present species greenish-cream to brown ones. *Eudistoma anaematum* does not have the shiny, spherical cells of the present species. Although the larvae of *E. pratulum* are not known, large embryos indicate the larval trunk could be at least 0.75mm long, i.e. similar to *E. muscosum* nom. nov.

Eudistoma purpureum n.sp.
(Fig. 86)

DISTRIBUTION

TYPE LOCALITY. Queensland (Wistari Reef, under rubble near reef edge, coll. P.Kott 1.11.86, holotype QM GH4466; 30.10.86, paratype QM GH4467; Heron I., January 1983, paratype QM GH4455).

FURTHER RECORDS: Queensland (Capricorn Group, QM G11972-6 GH4456-65 GH4481 GH4484 GH4491 GH4561 GH4567 GH4581 GH4585).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are sessile cushions, fixed by a flat base, rounded on the upper surface, usually 2 to 5cm in diameter and up to 2cm high. Only occasionally is the colony divided into 2 or 3 lobes arising from a common base. Living specimens are completely opaque, 'indian-purple' or 'hyacinth-blue' (Ridgeway 1886) in colour, the surface smooth and shiny. In preservative colonies are grey-black to cloudy-grey, and sometimes the test becomes translucent with darkly pigmented greenish-black zooids showing through it. Minute dark pigment cells are scattered through the test, but are especially concentrated around the zooids, and in the body wall. Also small cloudy crowded test cells confer a cloudy appearance especially evident in the upper layer of test.

Four to 6 zooids form circular systems with the atrial apertures opening in the centre of the circle. Zooid openings are relatively inconspicuous on the surface and no depressions or other marks are on the surface.

Sand is in the base of the colony and sometimes extends up into the centre of the base of the colony, but never reaches the upper half. Oval faecal pellets in varying quantities are in the test, which is gelatinous and soft but turgid.

INTERNAL STRUCTURE: Zooids are about 6mm long, and the thorax is relatively wide. The atrial siphon is often up to 3 times the length of the branchial siphon. Variable concentrations of minute dark pigment particles are in the body wall. There are about 12 longitudinal thoracic muscles and more numerous circular ones. Circular muscles are along each siphon.

In the pharynx is a fairly extensive prestigmatal zone, and about 20 stigmata in each row, the most ventral ones reducing in length. Dorsal stigmata in the anterior row also are reduced in length and the row curves anteriorly along the mid-line to reach up along each side of the neural ganglion.

There is the usual long oesophageal neck. The smooth-walled stomach is in the posterior end of the abdomen, and a long duodenal area, but the posterior stomach is not well defined and often the mid-intestine appears uninterrupted. The rectum originates in the pole of the gut loop. The gastro-intestinal gland consists of long tubules that branch from the main stem of the duct near its origin (at the pyloric end of the stomach), and extend around the rectum at a level with the stomach.

Gonads are found maturing in specimens collected in October and November. Male follicles are relatively large and pyriform, and a large ovum is at the side of the gut loop. The vas deferens is particularly conspicuous, dark-greenish in preservative.

One or 2 embryos are in the atrial cavity of specimens collected in late October (QM GH4467), November (QM GH4457 GH4466) and January (QM GH4455). Larvae are large, the trunk 1.5mm long, with the tail barely reaching to its anterior end. Large median ampullae alternate with the adhesive organs, and accessory ampullae arise as lateral bract-like expansions from the stalk of each adhesive organ. Larvae have 3 rows of stigmata, as do those of *E. maculosum* n.sp. and *E. purpureum* n.sp. Fine ectodermal projections into the larval test surround the apertures as in *E. ovatum* and other species (see Annotated Glossary: **larvae**).

REMARKS. Living, the species is distinguished by its brilliant, opaque, purple colour, smooth shiny surface and entire (rather than lobed) colony. Preserved specimens are distinguished by the absence of symbionts (present in *E. amplum*), smooth, round, sessile colonies, absence of any red or orange, and dark-greenish zooids. Muscles of the atrial and branchial siphons are not concentrated into a distinct bulging sphincter as in *E. angolanum* (see above) and sand is only sparse in the base of the colonies.

Tokioka (1967a) assigned specimens from the Marianas and Gilbert Is to *E. angolanum*. These specimens are diverse — some have embedded sand, others do not; some have vesicles in the surface test while others lack them and there are from 12 to 20 stigmata and 10 to 30 longitudinal muscles. The lack of characteristic siphonal sphincter muscles in any of Tokioka's specimens suggests these may not be conspecific with *E. angolanum*. The range in all characters recorded by Tokioka suggests his material represents more than one species. It could include specimens of *E. purpureum*. However, zooids are reported yellowish-orange or reddish-brown, the dark colour of the vas deferens is not described, and larvae have more numerous epidermal ampullae than the present species. Thus, at this stage *E. purpureum* cannot be positively regarded as

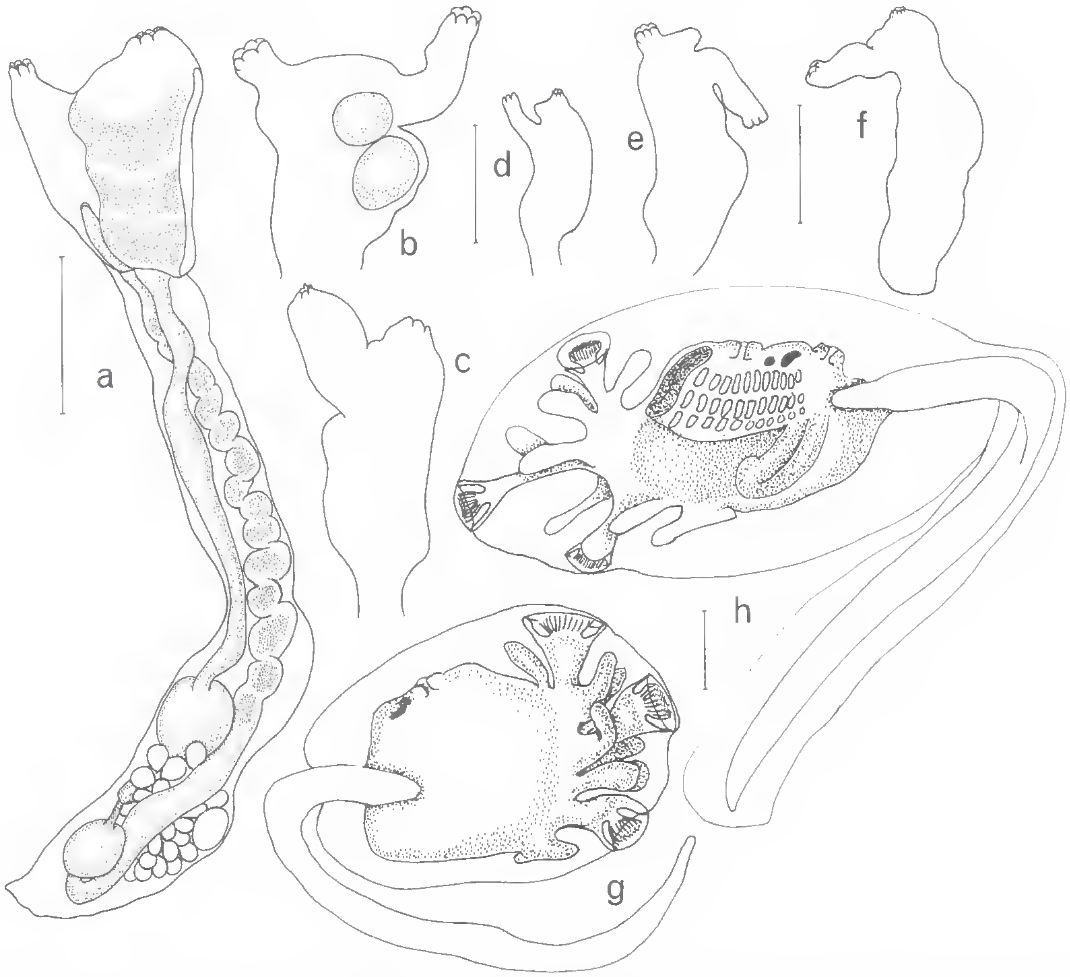


FIG. 86, *Eudistoma purpureum* n.sp.: **a**, zooid (paratype QM GH4467); **b–f**, thoraces showing various positions of the atrial siphon (QM G11974); **g,h**, larvae at successive stages of development (QM GH4457). Scales: **a–f**, 1mm; **g,h**, 0.2mm.

conspecific with any of the previously recorded species of the genus *Eudistoma*.

Eudistoma maculosum n.sp. (> *E. renieri*: Kott, 1957a) from Cockburn Sound has larvae with the same bract-like accessory ectodermal ampullae as the present species. However, its larvae are smaller and the colonies sheet-like with a distinctive colour pattern — although that is not conspicuous in the preserved material. *Eudistoma marianense* Tokioka 1967a also has similar larvae to those of the present species but it appears to lack the lateral ampullae.

Eudistoma pyriforme (Herdman, 1886)

(Fig. 87a)

Psammaphlidum pyriforme Herdman, 1886, p. 419.
Eudistoma pyriforme: Tokioka, 1950, p. 120. **Not** Kott 1957a, p. 75 (> *Eudistoma sabulosum* n.sp.); 1972b (> *E. aureum* n.sp.); 1976, p. 58 (> *Eudistoma sabulosum* n.sp. and *E. maculosum* n.sp.)

Distribution

New Records: Queensland (Bargara, QM GH4552).

Previously Recorded: Queensland (Torres Strait — Herdman 1886). Palau Is (Tokioka 1950).

Description

External Appearance: The colony has rather irregular, rounded to flat-topped lobes joined to common basal test. They are up to 2cm high, one to 2cm in diameter on the upper free surface, and they taper slightly toward the base. The test is packed with sand which obscures the circular systems, each of about 6 zooids, opening on the upper surface of the head. Zooids are white in preservative.

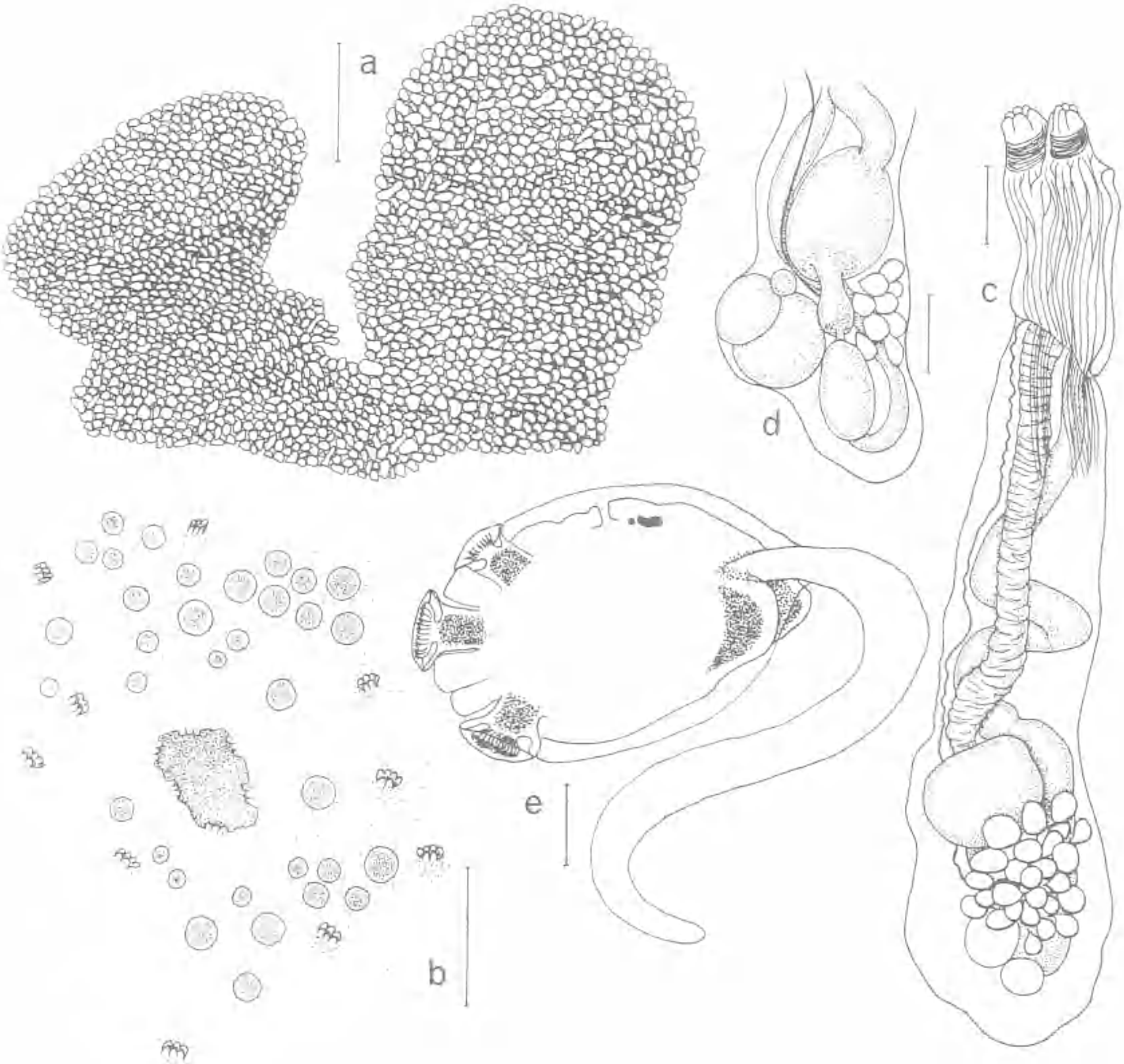


FIG. 87, *Eudistoma pyriforme* (QM GH4552): **a**, colony. *Eudistoma reginum* n.sp.: **b**, view of surface showing branchial apertures surrounding cloacal depression and vesicles in the test (QM G11951); **c**, zooid (QM GH4489), **d**, dorsal view of abdomen (QM GH4489); **e**, larva (QM GH4489). Scales: **a**, 5mm; **b**, 1mm; **c**,**d**, 0.5mm; **e**, 0.2mm.

INTERNAL APPEARANCE. Zooids are relatively small, about 2.5mm when contracted. They have 5 to 10 widely separated longitudinal muscle bands on the thorax, and these continue along the abdomen in a single wide band on each side. The atrial siphon is longer than the branchial siphon.

The gut has the usual rounded stomach, long duodenal area, and large oval posterior stomach. In contracted zooids, the intestine makes a horizontal loop across the abdomen behind the stomach.

There are no embryos in the newly recorded specimen (collected in May).

REMARKS. The present species is distinguished from other sandy species by its separate lobes, rather than flat, investing colonies. It resembles *E. globosum* to some extent — however, in the latter species, zooids are more crowded, are not in circles, colony lobes are more rounded than flat-topped, and the surface test over the head of the colony is always free of sand.

Eudistoma reginum n.sp.

(Fig. 87h–c. Plate 16e,f)

? *Eudistoma amplum*: Millar, 1975, p. 219 (part, specimen from Toeal with cloacal cavity).

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., on underside of rubble behind reef edge LWM, coll. P.Kott March 1975, holotype QM G11948; Heron I., coll. P.Kott September 1976, paratype QM G11950; Wistari Reef, coll. P.Kott July 1976, paratype QM G11949; Tryon Reef, coll. P.Kott September 1975, paratype QM G11951).

FURTHER RECORDS: Queensland (Capricorn Group, QM G11969 GH888 GH4447 51 GH4485 90 GH4492 GH4522 6 GH4580 GH4586; Lizard I., QM G11966).

DESCRIPTION

EXTERNAL APPEARANCE In life the colonies are 'aster purple' (Ridgeway 1886) and form smooth-surfaced cushions to sheets from about 3 up to 20cm (QM GH4524) in maximum extent and from 0.5 to about 2cm thick. Preserved they are brownish-orange, hard, flat and rather leathery. The preservative is stained a bright orange. The border of the colony is rounded and slightly raised above the upper surface. Sand is in the base of the test and in patches throughout, sometimes just beneath the upper surface. In some colonies a sandy border around each system is seen through the reddish-purple test. Occasionally sand grains are crowded. Small spindle-shaped dark pigment cells in the test immediately surround the zooids. Large (0.3mm diameter) vesicles are present at all levels through the test, particularly conspicuous (but never crowded together) in the upper surface between zooid openings. They contain crystalline material. Small, tan, soft-looking, opaque, pigment cells are crowded between the large vesicles. Oval faecal pellets are also in the test.

About 7 or 8 zooids are in each circular system. The systems are about 3mm in diameter. Most of the atrial apertures are close together around the edge of a depression in the centre of each system. Others open in the centre of the depression, and are not associated with its rim. The 3 anterior lobes of those atrial apertures around the edge of the depression are inserted into corresponding lobes of the test around the rim which projects inwards, over the depression, to form a lobed cloacal aperture over a rudimentary cloacal cavity.

INTERNAL STRUCTURE: Flecks of orange pigment in the body wall of zooids and embryos colour them orange. Zooids are robust but relatively short (about 4mm long contracted) and narrow with strong musculature consisting of about 20 longitudinal bands on the thorax. Circular muscles are more numerous forming an almost continuous coat. Circular muscles on the siphons are strong, evenly spaced along the length of the siphon, and not gathered into a distinct band. The posterior end of the abdomen often is found bent up sharply against the anterior part of the zooid.

Stigmata are about 16 in each row, but are difficult to count. The stomach is small and smooth, the duodenal area long. A large, oval, posterior stomach, separated from the rectum by a short constriction in the pole of the gut loop occupies most of the mid-intestine. Thin-walled terminal ampullae of the gastro-intestinal gland surround the rectum and duodenum in many specimens.

Gonads are a mass of pyriform follicles, with a large egg on the left side of the gut loop. Two or 3 embryos are in the atrial cavity of specimens collected in October and November (QM GH4448 GH4450). However, maturing gonads occur in May (QM GH888). Thus, it is possible there are two breeding seasons.

The larval trunk is 1mm long with a short tail, barely reaching the anterior end of the trunk. Larvae are unusual in having patches of brown pigment in the posterior horns of the haemocoel — one on each side of the base of the tail, and in the stalks of the adhesive organs. Ampullae are only in the mid-line between the adhesive organs, one between the 2 upper ones and 2 between the 2 lower ones.

REMARKS: Like others in the angolanum group, *E. reginum* has large vesicles in the test containing crystalline material, circular systems with a shallow, rudimentary cloacal cavity, anterior lobes of the atrial apertures inserted into the test around the perimeter of the cloacal cavity and folding inwards to form a rudimentary cloacal aperture, and unusual brown pigmentation in the larval haemocoel.

The species has much smaller cloacal systems, shorter siphons, usually less sand in the test, and shorter larval trunk than *Eudistoma carnosum* n.sp. *Eudistoma angolanum* has a red test packed with embedded sand, zooids with long, snake-like atrial siphons with a bulging sphincter muscle, and larvae with numerous lateral ampullae. *Eudistoma multiperforatum* (Sluiter, 1909) has tough investing colonies with red test, sand embedded in the basal half of the colony and preserved colonies resembling those of the present species; but its zooids are not arranged in circles, and the atrial siphons are short (see ZMA TU809.1, TU809.2).

Eudistoma muscosum nom. nov. also has dark pigment in the posterior horns of the haemocoel but lacks the cloacal cavities in the test.

Eudistoma sabulosum n.sp.
(Fig. 88. Plate 16g)

Eudistoma pyriforme: Kott, 1957a, p. 75 (part, specimens from Port Noarlunga); 1976, p. 58 (part, specimen from Western Port).

DISTRIBUTION

TYPE LOCALITY: South Australia (Topgallant I., 5m, coll. N. Holmes 29.3.82, holotype QM GH937; Ward I., 1-5m, coll. N. Holmes 31.3.82, paratype QM GH4591).

FURTHER RECORDS: South Australia (St. Vincent Gulf, QM GH4588). Victoria (off Lakes Entrance QM GH4587; Bass Strait, MV F54583, QM G11864 GH4589; Western Port, MV F53405, QM GH4590).

PREVIOUSLY RECORDED: South Australian (St. Vincent Gulf — AM Kott 1957a). Victoria (Western Port — MV Kott 1976).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are sessile rounded to irregularly-shaped cushions with rounded borders, up to 4cm in diameter and 2cm thick. Colonies are solid. The test, especially in the outer layers, is packed with sand which dominates the colour of the colony. The upper surface, subdivided into protuberant, rounded swellings, resembles a cauliflower. Zooids are in circular systems, about 5 per system. The atrial apertures in the centre of the circle open onto slight conical elevations. The branchial apertures are in depressions around the base of these elevations.

Between the sand, the test is colourless in preserved specimens. Abdomina of the crowded zooids criss-cross one another, but thoraces lie parallel, with only thin layers of test separating them. Thus, when the zooids are contracted, the upper layer of the colony has a rather loose consistency. The crowded sand makes the test hard, enclosing rigid compartments that contain the zooids.

INTERNAL STRUCTURE: Zooids are relatively small and muscular. Short and inconspicuous sphincters are around the apertures. The atrial siphon is longer than the branchial siphon. There are about 30 longitudinal thoracic muscles and an almost continuous layer of circular muscles. Stigmata are only 8 to 10 per row. The gut has the usual smooth, round stomach, long duodenal area, and oval posterior stomach. In contracted individuals, the intestine forms an S-bend or horizontal loop just posterior to the level of the stomach. Sometimes the whole posterior end of the abdomen is bent up against the zooids. Up to 6 embryos are in the atrial cavity of specimens collected in January (Kott 1957a). The larvae are small, the trunk being 0.5mm long. The tail is wound three-quarters of the way around it. Adhesive organs have long, narrow stalks. There are 2 pairs of long lateral ectodermal ampullae, and unpaired ampullae dorsal and ventral to the adhesive organs in the mid-line, but no median ampullae alternating with adhesive organs.

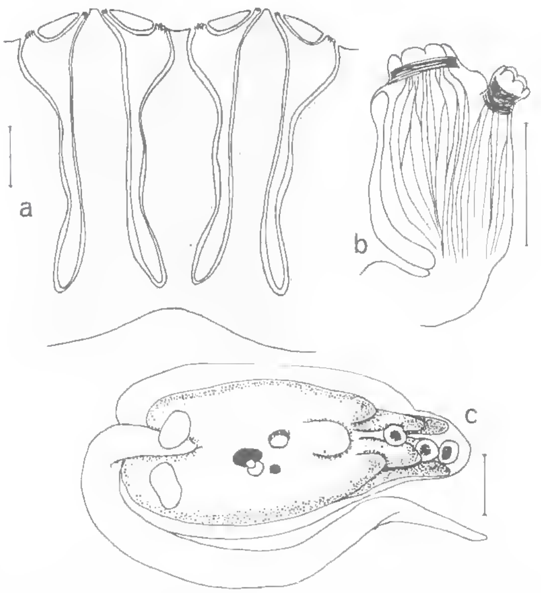


FIG. 88, *Eudistoma sabulosum*, n.sp.: **a**, section through colony showing arrangement of zooids (holotype QM GH937); **b**, thorax (QM G11864); **c**, larva, dorsal view (QM GH4588). Scales: **a**, 2mm; **b**, 0.5mm; **c**, 0.1mm.

REMARKS: The species is distinguished from the tropical *Eudistoma ovatum* by its irregular, cauliflower-like upper surface, the slight conical elevations supporting the atrial apertures above the surface of the colony, and its smaller zooids with only about 10 stigmata. Zooids of both species contract in much the same way, with, in extreme cases, the abdomen folded up against the rest of the zooid. Larvae of both species are small, although the tropical *E. ovatum* has median as well as lateral ampullae, while the present species lacks the median ampullae that alternate with the adhesive organs.

Eudistoma constrictum n.sp., another sandy species from temperate Australian waters, lacks the circular systems of the present species and has a much larger larva.

Eudistoma superlatum n.sp.
(Fig. 89)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Shark Bay nr. South Passage, 10-15m, coll. L. Marsh 8.4.79, holotype WAM 822.83 *QM GH2136*; Abrolhos Is, Easter Group, coll. P. McMillan 16.5.63, paratype WAM 189.75).

FURTHER RECORDS: Western Australia (Montebello Is, WAM 770.83; ? Port Hedland, WAM 769.83; Houtman's Abrolhos, WAM 768.83).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype colony is massive and fleshy, 8cm long, 6cm wide at the base, and 6cm high. It is fixed to the substrate by the whole of the base. The upper part is divided into 10 lobes, each lobe oval in section. No zooid systems are formed. The test is firm and gelatinous, more or less opaque and crowded with cloudy cells that are pinkish-beige in preservative. Zooids are crowded, pink in preservative, and both openings are in inconspicuous circular areas of thin test all over the outer surface of the lobes and the sides of basal half of the colony. The outer surface of the colony is completely naked, and although faecal pellets are embedded in the test, there is no sand. The paratype colony is a single oval head about 5cm long and 4cm in diameter with a short, thick fleshy stalk.

INTERNAL STRUCTURE: Zooids are up to about 2cm long. They are slender and have a long, delicate, posterior abdominal vascular extension. When contracted the gut is folded up into a wide loop that projects from the side of the abdomen. However, in extended zooids there is the usual long oesophageal neck. Both apertures are at the anterior end of the zooid. The atrial opening is sometimes on a long siphon, but the branchial aperture is almost sessile. About 20 fine longitudinal muscle bands are on each side of the thorax. These continue along the abdomen in about 3 wide bands which converge into a small, pointed projection on each side of the base of the muscle-free vascular stolon. About 40 fine, transverse muscles on the thorax, form a fine mesh with the longitudinal muscles.

The branchial tentacles are in at least 3 rows. The prestigmatal area of the pharynx is only shallow. The anterior row, which inclines forwards along each side of the mid-dorsal line has 34 long stigmata, 26 in the middle row, and about 24 in the posterior row. The small, smooth stomach, long duodenal area, and oval posterior stomach are all in the posterior end of the abdomen as is usual for the genus.

No gonads were detected in the holotype, although they are present in the gut loop in the paratype, which also has a single embryo in the atrial cavity — protruding slightly from it in these contracted specimens. The delicate and long, posterior vascular stolon in this species may be associated with the large size of the colony.

REMARKS: Although *Eudistoma* contains species with extensive sheet-like colonies, it has

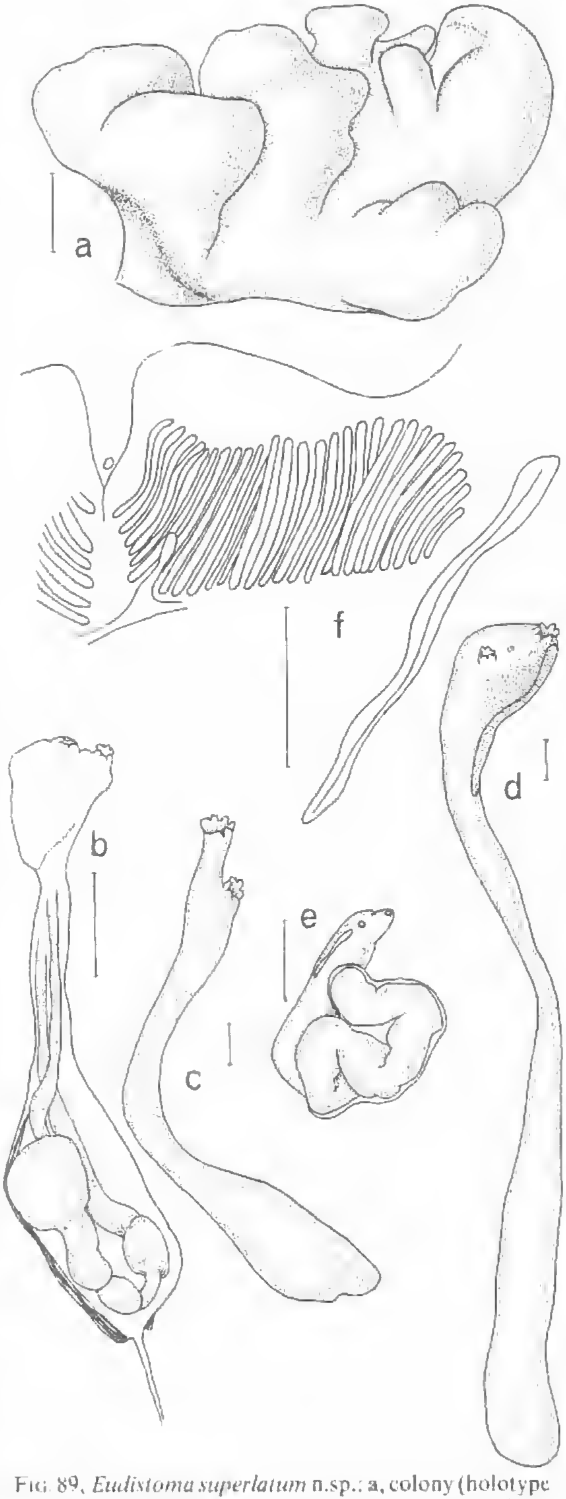


FIG. 89, *Eudistoma superlatum* n.sp.: a, colony (holotype WAM 822.83); b–e, zooids (holotype QM GH2136); f, first row of stigmata on left side. Scales: a, 2cm; b–e, 1mm; f, 0.5mm.

few species with massive, bulky and fleshy lobed colonies like the present species. In this, the species resembles *Sigillina* spp. and *Pseudodistoma* spp. *Sigillina fantasiana* and *S. nigra* resemble the present species in lacking the usual sigillinid muscle fibres and epicardial extension respectively on and in the vascular stolon. However, zooids of the present species are smaller than those of *Sigillina* spp., and they have the longer oesophageal neck of *Eudistoma*. The heart is at the posterior end of the abdomen, rather than in the posterior abdominal extension as it is in *Pseudodistoma*. *Eudistoma glaucum* is the only other known species of *Eudistoma* with a long vascular stolon, although it is not as long as in the present species.

The regular arrangement of zooids, without circular systems, resembles that of the stalked species *Eudistoma globosum* and *E. elongatum* and a few sandy species (*E. constrictum* n.sp. and *E. microlarvum* n.sp.).

This large, fleshy colony, with its characteristically eudistomid zooids and long, delicate vascular stolon, is readily distinguished from other species of the genus.

The colony from Port Hedland recorded above is long and rope-like, and although its zooids seem to be the same as the type material, they are badly mutilated and the identification needs confirmation.

Eudistoma tigrum n.sp.

(Fig. 90)

Eudistoma rigida: Kott, 1981, p. 151.

DISTRIBUTION

TYPE LOCALITY. Queensland (Heron I., rubble fauna, coll. P. Kott, August 1975, holotype QM G11941; Wistari Reef, low water mark, rubble zone, coll. P. Kott August 1975, paratypes QM G11942-4; Wistari Reef, coll. P Kott 6.8.82, paratype QM GH1362.

FURTHER RECORDS: Western Australia (Houtman's Abrolhos, QM GH2135, WAM 839.83). Queensland (Hervey Bay, QM GH4559-60; Capricorn Group, QM G11943 GH1354 GH1362 GH4518-9). Fiji (Kott 1981).

DESCRIPTION

EXTERNAL APPEARANCE: Firm, gelatinous colonies are circular, oval or slightly irregular cushions or sheets, up to 5cm long and from 0.5 to 1.5cm thick, with a smooth, sand-free surface. They are fixed by the whole of the basal surface.

In life more or less circular patches of black or 'gallstone-yellow' (Ridgeway 1886) pigment are in the surface test. These patches, up to about 0.5cm in diameter, are separated by broad (about 2 to 3mm wide) areas of grey or white test. In preservative the whitish areas become reddish-brown, rust coloured or brownish-yellow, the pigment contained in spherical pigment cells 0.02 to 0.03mm in diameter. The darker pigment, contained in irregularly shaped cells, fades in preservative and the patches that were darkly pigmented in life become translucent. The colour pattern is confined to the surface test, and the remainder of the test is cloudy and translucent. A little sand is embedded in the basal test, but absent elsewhere. Faecal pellets are in the test.

Zooids are in circular systems of 5 or 6 zooids. The systems are independent of the pigment patches, and are about 2mm in diameter. In freshly preserved zooids the stomach and the proximal part of the intestine are green.

INTERNAL STRUCTURE: Zooids are robust, but only about 4mm when contracted, and up to 8mm when extended. Strong circular muscles surround each siphon. The atrial siphon is often long, about 3 times the length of the branchial siphon. About 20 longitudinal muscles are on the thorax, extending onto the adbomen in 2 or more bands. The inner layer of circular muscles on the thorax is thin, but forms an almost continuous coat of at least 25 bands. Branchial tentacles are in 3 circles of about 12 or more. Only a fairly shallow unperforated area of pharynx is anterior to the stigmata. Stigmata are 18 in the posterior row, 22 in the next row, and about 24 in the anterior row (which inclines forwards along each side of the mid-dorsal line).

There is the usual small smooth-walled stomach in the posterior end of the abdomen. A long almost elliptical posterior stomach is in the posterior end of the descending limb of the gut loop. Long tubules of the gastric gland extend anteriorly along the ascending limb of the gut loop, level with the duodenal area, and a mass of vesicles surrounds the duodenal area.

One or 2 relatively large embryos are in the atrial cavity of specimens collected in March (QM G11943), but not in July or August. The larval trunk is 0.75mm long, and the broad tail curves up across the left side of the anterior end of the trunk at the base of the ampullae, and then continues posteriorly along the mid-dorsal line, reaching to about three quarters of the distance along the dorsal border. Large median ectodermal ampullae alternate with the 3 stalked adhesive organs in the anterior mid-line. The stalks of the adhesive organs are thin, but not long, and there is a circular knob of adhesive cells in a shallow epidermal cup.

REMARKS: The pigment pattern in this species resembles that of *E. maculosum* n.sp. which is distinguished by its larger larva with bract-like

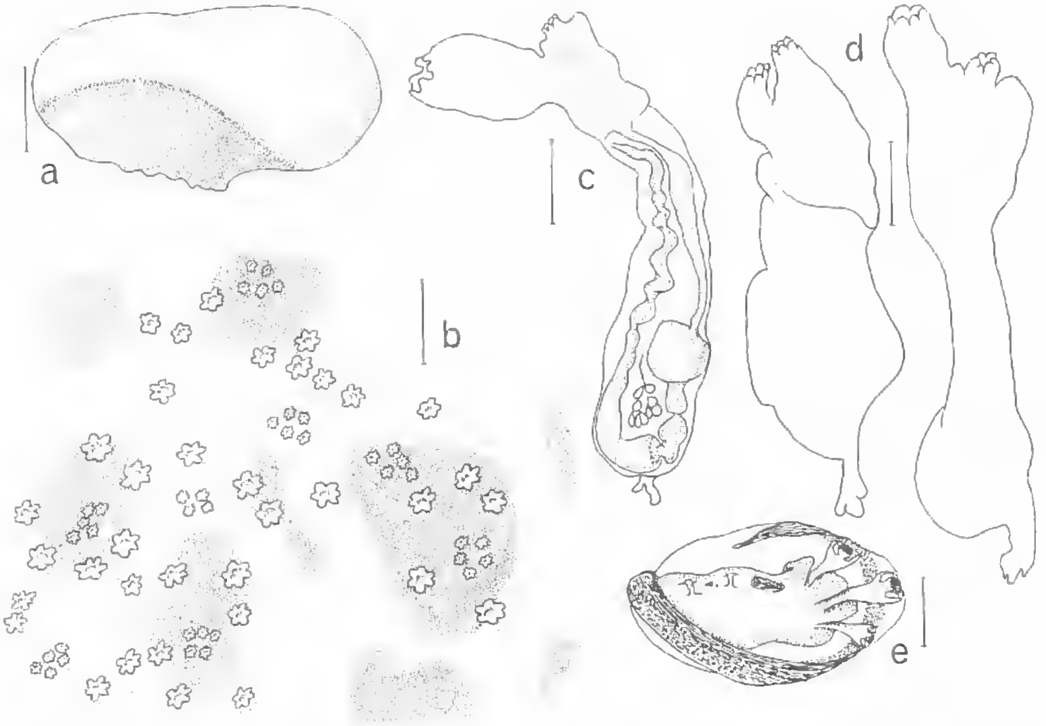


FIG. 90, *Eudistoma tigrum*, n.sp.: **a**, colony (QM G11943); **b**, arrangement of zooids, showing circles of small atrial openings in the centre of irregular circles of the larger branchial openings (QM GH1354); **c,d**, zooids, showing various positions of atrial siphon (QM G11942 GH1354); **e**, larva (QM G11943). Scales: **a**, 1cm; **b**, 2mm; **c,d**, 0.5mm; **e**, 0.2mm.

ectodermal ampullae that embrace the base of each adhesive organ and the long, enlarged platforms of adhesive cells. The pigment pattern is less conspicuous in preserved material, although large dark pigment cells and smaller tan ones persist for a long time in preservative. *Eudistoma muscosum* nom. nov. has a regular cushion-like colony, brownish-red zooids with a large spherical mass of male follicles, spherical brown-red pigment cells (0.03 to 0.04mm in diameter) and a larger larva (trunk 1mm long) than the present species. *Eudistoma purpureum* n.sp., also has rounded cushion-like colonies rather than the more extensive sheets of the present species, a dark vas deferens, and its larvae (trunk 1.5mm long) are larger than those of the present species.

Larvae, with their broad tails curving around on the left side of the larval trunk, resemble those of *E. gilboviride*, although the ampullae are different.

Colonies, zooids and larvae of specimens from Fiji assigned to *E. rigida* by Kott (1981) are identical with the present species. Specimens from French Polynesia provisionally assigned to *E. rigidum* by Monniot and Monniot (1987) have smaller colonies and smaller larvae (less than 0.5mm) and do not appear to be the same as the Fijian or Australian material.

Eudistoma tumidum n.sp.
(Fig. 91)

Eudistoma ovatum: Kott, 1972e, p. 43 (part, specimen from St. 27).

DISTRIBUTION

TYPE LOCALITY: Gulf of Carpentaria, 16°52.7'S, 140°56.2'E, Station 27 CSIRO Prawn Survey, 5.8.1963, holotype, AM Y1068.

DESCRIPTION

EXTERNAL APPEARANCE: The single colony available is more or less dome-shaped, about 6cm in diameter, consisting of a number of lobes of one to 2cm diameter arising from a common basal test mass. Although the preserved specimen is distorted and hardened and the rounded lobes of the upper surface are flattened, in life they probably were rounded and when inflated the colony probably appeared as an entire hemispherical mass, its separation into discrete lobes becoming obscured. The preserved specimen is grey and colourless, without sand, either on the surface or embedded on the test. However, the centre of each lobe, and of the colony, is packed with faecal pellets. Zooids are crowded and open all around the surface of the lobes. The arrangement of zooids could not be determined in this distorted specimen. However, the long atrial siphon suggests that they are arranged in circles with the atrial apertures in the centre of each circle.

Internal Structure: Zooids are robust. Contracted thoraces are only about 1mm long but they are also relatively thick. About 20 longitudinal muscle bands on the thorax continue along the ventral border of the abdomen. On the thorax the longitudinal bands overlie about 30 distinct bands of transverse muscle. There are 3 rows of branchial tentacles, those in the posterior row being relatively long. The dorsal end of the first row of stigmata inclines anteriorly along each side of the dorsal mid-line. There are at least 20 stigmata in the anterior row, but these could not be counted accurately. The longitudinal muscle bands continue along each side of the long abdomen, which has the usual smooth eudistomid stomach at its posterior end. The male and female gonads are in their usual position in the posterior end of the gut loop.

This specimen, collected in August, has up to 4 developing embryos in the peribranchial cavity. The larval trunk is 0.5mm long, and the tail is wound almost three-quarters of the way around it. A large cerebral vesicle has an otolith, and an ocellus with conspicuous lens cells. Adhesive organs are relatively small, each with an axial cone in its epidermal cup at the end of a long, slender stalk. Each of 4 long, pointed lateral ectodermal ampullae on each side of the anterior end of the trunk has a parietal branch from its base. The parietal branches also come to a point anteriorly but are rounded posteriorly. There are no median ampullae.

Remarks: The species is characterised by its naked, lobed colony with the zooids in circles, and by its larvae with parietal lobes at the base of the exclusively lateral ampullae.

Eudistoma laysani also has naked, lobed colonies with crowded zooids, but the lobes are smaller, zooids are not in systems, and both zooids and larvae are smaller than those of the present species. *Eudistoma gilboviride* also has lobed colonies and separate transverse muscle bands rather than a continuous coat. However, the lobes of *E. gilboviride* are top-shaped, its pigmentation is conspicuous and persists for a long time in alcohol, its zooids are not crowded, and larvae are much larger than those of the present species and lack the parietal lobes at the base of the lateral ampullae.

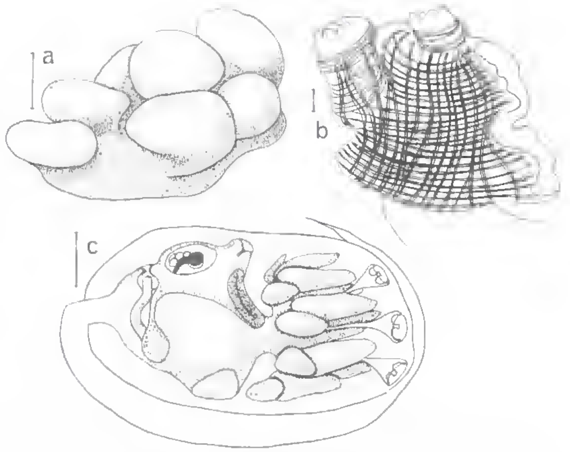


Fig. 91, *Eudistoma tumidum* n.sp. (holotype AM Y1068): **a**, colony; **b**, thorax showing muscles; **c**, larva. Scales: **a**, 1cm; **b**,**c**, 0.1mm.

Although both zooids and larvae are similar, Kott (1972e) was in error in assigning this specimen to *E. ovatum*. The latter species has extensive, smooth-surfaced colonies without lobes, and with embedded sand. Its larvae differ in that, although there are 2 lateral ampullae with parietal branches on each side, the dorsal and ventral ampullae are median (albeit with a parietal branch on each side) and the tail is slightly shorter than that of the present species.

The lectotype (ZMA TU1268) of *Eudistoma segmentatum* (Sluiter, 1909) also has the centre of each lobe of the colony packed with faecal pellets. However, zooids open at the free ends of long cylindrical stalks (rather than around convex sessile lobes arising from the common basal test, the thoracic transverse musculature is in a continuous coat (rather than in separate bands forming an open mesh with the longitudinal muscles), and both atrial and branchial siphons are short (in the present species the atrial siphon is long).

Genus **Exostoma** n.gen.

Type species: *Polycitor ianthinus* Sluiter, 1909.

The genus is monotypic. It has 6-lobed branchial and atrial apertures, on well developed muscular siphons. The atrial siphon is posteriorly positioned, and opens into an extensive cloacal cavity. Longitudinal muscle bands extend from the thorax along the abdomen in a band each side of the ventral line. A conspicuous layer of transverse thoracic muscles lies beneath the longitudinal bands. There are 3 rows of stigmata without parastigmatic vessels. The oesophageal neck is long, and the smooth stomach is in the posterior part of the long abdomen. Only short vascular processes arise from the posterior end of the abdomen.

Although Sluiter (1909) did not record the presence of a cloacal chamber in his description of *Polycitor ianthinus*, his figure (pl VIII, fig. 3) clearly shows the aperture at the top of the colony.

In its extensive cloacal cavity, posteriorly positioned 6-lobed atrial siphon, and 3 rows of stigmata the genus resembles species in *Hypodistoma*. However, zooids of the new genus are characteristic of the Polycitoridae rather than the Holozoidae, being long, with a long oesophageal neck, short vascular processes, and brooding their embryos in the atrial cavity (rather than in a brood pouch). The 3 larval adhesive organs are in the median line and have a wide flat-topped tuft of axial columnar cells in a deep epidermal cup, as in *Eudistoma*.

The genus *Hypodistoma* Tokioka, 1967a, defined by its type species *Distoma deerratum* Sluiter, 1895 from northern Australia, is a genus of the Holozoidae (related to *Sigillina*) which includes *H. vasta* (Millar, 1962) from South Africa. However, *Hypodistoma vastum*: Tokioka, 1967a from the Palau Is is a junior synonym of *Polycitor ianthinus* — the type species of the present new genus, *Exostoma*.

It seems the presence of a cloacal cavity, a unique feature in the Polycitoridae, is a development in parallel with the development of a similar colony form in the Holozoidae, and the similar position of the atrial siphon is a convergent adaptation associated with the presence of the extensive cloacal cavity. Phylogenetically, the new genus appears most closely related to *Eudistoma*, with its long oesophageal neck, 3 rows of stigmata and conspicuous transverse thoracic muscle bands beneath the longitudinal bands.

The only known species has a tropical western Pacific range.

Exostoma ianthinum (Sluiter 1909)

(Fig. 92)

Polycitor ianthinus Sluiter, 1909, p. 20. Van Name 1918, p. 135.
Hypodistoma ianthinum: Millar, 1975, p. 217.
? *Polycitor torosus* Sluiter, 1909 p. 18.
Hypodistoma vastum: Tokioka, 1967a, p. 126, Nishikawa, 1984, p. 121.
Not *Sigillina vasta* Millar, 1962, p. 153.

DISTRIBUTION

NEW RECORDS: New Guinea (Motupore I. QM GH235). Philippines (QM GH495).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1909 Millar 1975). Philippines (Van Name 1918). Palau Is (Tokioka 1967a).

The species has not yet been recorded from Australia, although its occurrence off Port Moresby is not far removed from the north eastern Australian continental shelf and probably it occurs there. It was taken in sea grass beds at Motupore I. and has been recorded down to 150m (Van Name 1918).

DESCRIPTION

EXTERNAL APPEARANCE: The colony varies from an irregular cushion up to 3cm thick, fixed by a large part of its base, and with 3 or 4 large common cloacal openings on the upper surface, to an upright cone with a single large terminal cloacal aperture. The test is firm, although the outer layer is separated from the inner core by the extensive interconnecting cloacal spaces that are 2 to 3mm below the surface. The surface of the colony has wide rounded ridges and swellings that are generally oriented along radii that converge toward the cloacal apertures. The branchial apertures of the zooids open in the depressions between these ridges and swellings. In preservative colonies are always a dark purplish-brown colour.

INTERNAL STRUCTURE: Contracted zooids are about 1cm long, the greater part of their length being the long polycitorid oesophageal neck. The 6-lobed branchial aperture is terminal. There is a relatively long atrial siphon from the postero-dorsal corner of the thorax, and in relaxed zooids it is directed posteriorly. Although in contracted zooids it is often found directed anteriorly, this could result from the contraction of the zooids and their withdrawal from the surface of the colony. Zooids are in crowded groups curving across the top and around the sides of the cloacal spaces beneath the surface of the colony. Their 6-lobed atrial apertures on the end of the long siphons open into the roof or outer wall of the cloacal cavities.

The body musculature consists of numerous, but fine, longitudinal and transverse bands. Longitudinal muscles extend down the branchial siphon in 6 groups, one corresponding to each lobe around the rim of the aperture. About 20 longitudinal bands are on each side of the thorax. These continue as a pair of wide bands along the length of the abdomen, one each side of the mid-ventral line. Sphincters surround each of the apertures and the anterior part of the pharynx in front of the perforated area. About 30 circular muscles are fairly evenly spaced along the whole length of the thorax. Other circular and longitudinal bands extend along the whole length of the long atrial siphon.

At the base of the branchial siphon are 3 particularly robust tentacles, one on each side and one in the mid-ventral line. These alternate with 2 smaller tentacles in a circle slightly anterior to the larger ones. Rudimentary tentacles alternate with the larger sizes. The opening of the neural duct is directed forwards. The pointed dorsal languets are found slightly to the left of the dorsal mid-line. An extensive unperforated part of the pharyngeal wall exists anterior, and another posterior, to the perforated area which has 3 rows, each of 20 long stigmata.

The oesophagus is long, the smooth shield-shaped stomach is in the posterior end of the abdomen. The duodenal area is fairly long, and is sharply constricted from an oval posterior stomach. The narrow mid-intestine curves around in the pole of the gut loop. It enters the rectum at the proximal end of the descending limb. There

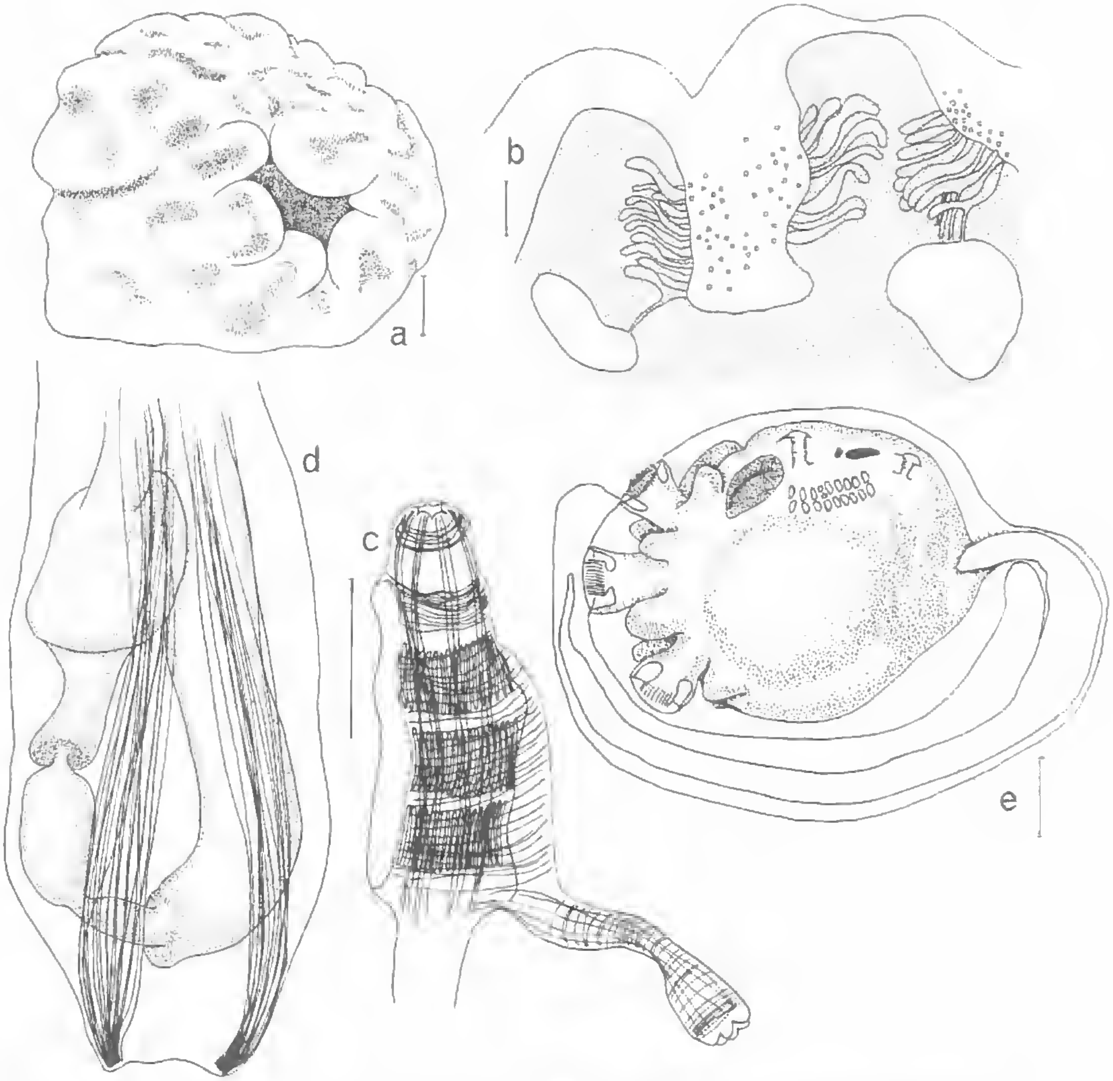


FIG. 92. *Exostoma ianthinum* n.gen. (QM GH235): **a**, colony; **b**, section through colony showing branchial openings of zooids into surface depressions, and long atrial siphons opening into cloacal canals; **c**, thorax; **d**, abdomen; **e**, larva. Scales: **a**, 1m; **b**, 2mm; **c**,**d**, 0.5mm; **e**, 0.2mm.

is a branched gastro-intestinal gland, but no reservoir.

The male gonad consists of a clump of almost spherical follicles on the right side of the gut loop in the vicinity of the stomach. A group of up to 3 large eggs are on the outside of the male follicles. A single ovum is incubated in the right peribranchial cavity anterior to the atrial siphon. Embryos are in the atrial cavity of the New Guinea specimen (collected in November). In the Philippine specimen, collected in July, tailed larvae are present. The larval trunk is 0.8mm long and the tail relatively short, being wound only half-way around the trunk. The 3 large adhesive organs, on short, thick stalks, are in the median line and alternate with paired ectodermal ampullae. The oozooid has 2 rows of stigmata.

Only short, inconspicuous vascular appendages are at the posterior end of each zooid.

REMARKS: Although the colony and to some extent zooids of this species resemble those of *Hypodistoma*, the zooids differ in having a long oesophageal neck, a small eudistomid-shaped stomach, and short, inconspicuous vascular appendage; and lacking a stalked brood pouch. Zooids are characteristic of the Polycitoridae. The species differs from *Eudistoma* spp. in having extensive cloacal systems.

Further, larvae resemble those of certain *Eudistoma* spp. (see *E. maculosum* n.sp.) with large adhesive organs on short, thick stalks.

Hypodistoma vastum: Nishikawa, 1984 from the western Pacific may be a synonym of the present species. Nishikawa (1984) believed it to be conspecific with *H. vastum*: Tokioka, 1967b, and with *H. ianthinum*: Millar, 1975, which are both synonyms of *Exostoma ianthinum*. However, he also included *Hypodistoma vastum* (Millar, 1962) in his synonymy. Since the latter species is a member of a different family and genus, its inclusion amongst the synonyms of Nishikawa's specimen raises doubts as to the identify of that specimen.

Polycitor torosus Sluiter, 1909, appears a cushion-like specimen of the present species. Although Sluiter regarded the gut loop as relatively short, this was probably only apparent, owing to the contraction of the abdomen, for relaxed zooids are reported about the same length as those of the present species.

Genus **Brevicollus** n.gen.

Type species: *Brevicollus tuberatus* n.gen. n.sp.

The genus is characterised by its relatively short, embedded zooids with separately opening 6-lobed apertures, 5 rows of stigmata, each row crossed by a parastigmatic vessel, and a short oesophageal neck. The stomach wall has longitudinal folds. Gonads, present in the end of the gut loop, consist of relatively large and numerous pyriform male follicles and a 5- or 6-egg ovary. Numerous (up to 12) embryos are brooded in the atrial cavity. The proximal part of the oviduct runs a convoluted course over the surface of the ovary. The body musculature consists of longitudinal bands that exchange fibres with one another to form a meshwork over the sides of the thorax before extending down the length of the abdomen. There are no transverse or oblique muscles.

The 3 deep, tulip-shaped, sessile larval adhesive organs in the anterior mid-line of the trunk are unique. These are surrounded by numerous ectodermal ampullae that project from the anterior end of the trunk. Also fine thread-like extensions from the ectodermal cells expand into tear-shaped vesicles at the surface of the test as in species of *Sigillina*, *Polycitor* and *Eudistoma* (see Annotated Glossary: **larvae**).

Polydistoma, a new genus of the Holozoidae also with 5 rows of stigmata, is distinguished from *Brevicollus* by its holozoid vascular stolon and brood pouch. The two known species of *Polydistoma* lack parastigmatic vessels, although these are in other holozoid genera (*Distaplia*, *Hypsistozoa* and *Neodistoma*). In view of other differences, the presence of parastigmatic vessels in *Brevicollus* rather than being indicative of common ancestry with the Holozoidae, probably is due to convergence, as there is no other evidence of any phylogenetic relationship.

Brevicollus has been assigned to the Polycitoridae because of its short vascular appendages, separately opening zooids, and absence of a posterior abdomen with gonads. However, it has some characters that are not shared with polycitorids, *viz.* a relatively large thorax, parastigmatic vessels in the branchial sac, a short oesophageal neck and a large number of embryos. Further, although the larval adhesive organs are in the anterior mid-line these sessile, tulip-shaped organs are unique. It is possible these anomalous characters are secondary adaptations that would not preclude a relationship with the Polycitoridae. The convolutions of the vas deferens could be associated with a secondary shortening of the abdomen. Another alternative for *Brevicollus* is an affinity with euherdmaniinid genera, since it differs from *Ritterella* only in its larva, convoluted vas deferens and lack of a posterior abdomen containing the gonads.

Thus, although, at present the genus is classified in the Polycitoridae on the basis of separately opening apertures, and lack of a posterior abdomen and long vascular stolon, it is possible the phylogeny of this new genus would be more accurately represented by an independent status reflecting a relationship with *Ritterella*.

This monotypic genus is at present known only from 2 specimens, one from each of two locations in southern Australia.

Brevicollus tuberatus n.sp.
(Fig. 93. Plate 16h)

DISTRIBUTION

TYPE LOCALITY: South Australia (The Gap, 15-20m, coll. N. Holmes and S. Shepherd 9.4.87, holotype SAM E2059 *QM GH4188*). Victoria (Gabo I., 10-15m, coll. J. Watson 14.5.70, paratype MV F45284 *QM GH4952*). FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The holotype colony is firm and tuber-like, growing along a weed stalk. The colony is basically a thick, undulating cylinder, randomly constricted along its length to partially separate it into short potato-shaped masses from 2 to 5cm long and about 2cm in diameter. The more angular lobes (4) of the paratype colony articulate with one another along the stalk of a *Pyura australis*. A thin layer of sand is on the surface, and also scattered evenly, but sparsely, through the firm, gelatinous, internal test. Zooids open all around the surface of the colony and converge toward the centre.

INTERNAL STRUCTURE: Zooids are relatively large, about 1cm long with a wide thorax. Both 6-lobed apertures are on the anterior end. Thorax and abdomen each occupy about half the length of the zooid. Strong circular muscles surround each aperture. Siphons are short. Longitudinal muscle bands from each siphon radiate out onto the thorax where they exchange fibres with one another to form a meshwork. They continue on to the abdomen as fine bands along its length. Five rows of 35 long rectangular stigmata are on each side of the branchial sac. Each row is crossed by a parastigmatic vessel; and is interrupted in the dorsal mid-line by the large dorsal sinus. Transverse branchial vessels continue over the dorsal sinus where each is produced into a narrow,

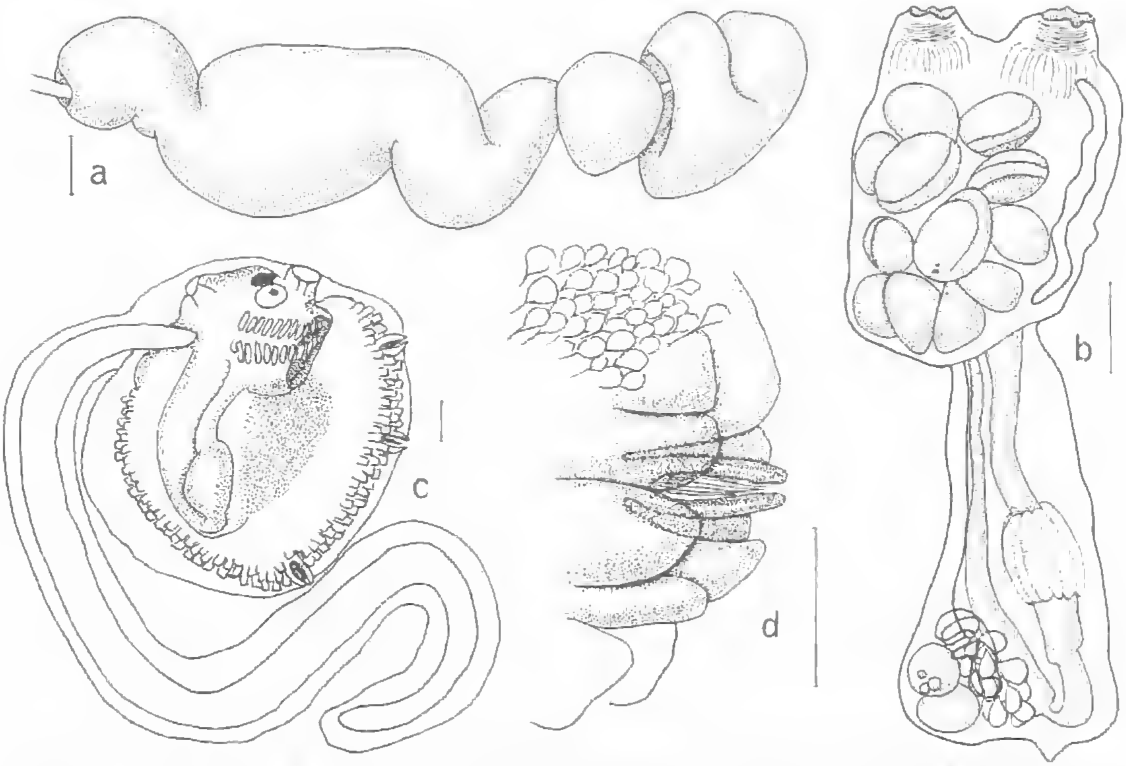


FIG. 93, *Brevicollus tuberatus*, n.gen., n.sp. (holotype SAM F2059, *QM GH4188*): a, colony; b, zooid; c, larva, epidermal vesicles not shown; d, anterior end of larval trunk, test removed from all but a small section, taking vesicles with it, to expose one of the unusual adhesive organs surrounded by epidermal ampullae. Scales: a, 1cm; b, 1mm; c,d, 0.1mm.

pointed, dorsal languet. Smaller languets occur where the parastigmatic vessels cross the dorsal sinus.

The oesophagus is relatively short. The rather small, shield-shaped stomach is in the middle one-third of the abdomen. It has 8 broad, rounded, longitudinal folds in its wall. A long elliptical posterior stomach is in the posterior third of the descending limb of the gut loop. The wide rectum extends from the pole of the gut loop to about halfway up the thorax, terminating in a 2-lipped anus. Gonads are in the posterior end of the gut loop overlapping the pole of the loop on the right side. The testis consists of about 25 pyriform follicles and the ovary contains up to 4 eggs, one or two larger than the others. The proximal end of the male duct runs a complex, convoluted course as it leaves the testis, sometimes becoming intermingled with the male follicles, then curving around onto the outer surface of the ovary before it straightens out to run alongside the rectum. It opens in the atrial cavity near the anus.

In this colony about 12 large, orange embryos are at various stages of development in the right peribranchial cavity. The trunk of the tailed larva is about 1mm long and is deeper than long. The oozooid is vertical, with a well formed branchial sac and gut loop. The former has 2 rows of stigmata. The atrial aperture is directed horizontally at right angles to the branchial aperture (unlike *Eudistoma* spp.). There is a large otolith and ocellus and the tail is wound completely around the trunk. The almost sessile adhesive organs are in a vertical line down the centre of the anterior end of the trunk. They consist of a deep tulip shaped cup with filamentous lamellae in the concavity. Numerous, crowded ectodermal ampullae project from the anterior larval epidermis. These, together with masses of tear-drop-shaped terminal vesicles attached to thread-like extensions of the ectodermal cells of the ampulla, obscure the adhesive organs. The whole front and ventral mid-line of the trunk has a foamy appearance resulting from these ampullae and their vesicles.

REMARKS: The larval adhesive organs of this species are in a vertical line, as in *Eudistoma* and *Polycitor*, but they are different, lacking the central axial cells. Further, the ectodermal ampullae are unusual, more numerous and crowded than in other species of the Polycitoridae. Although the ectodermal vesicles do occur in *Eudistoma* spp., they are not unique to the Polycitoridae, but occur in most other taxa (see Annotated Glossary: **larvae**) and are not indicative of relationships. These factors, together with the presence of parastigmatic vessels, a convoluted vas deferens, and the large number of larvae being incubated, distinguish the genus and the species from others in this family.

Polycitor obeliscus, also from South Australian waters, has 6 rows of stigmata. However it has other characters, in addition to the generic ones, which distinguish it from the present species.

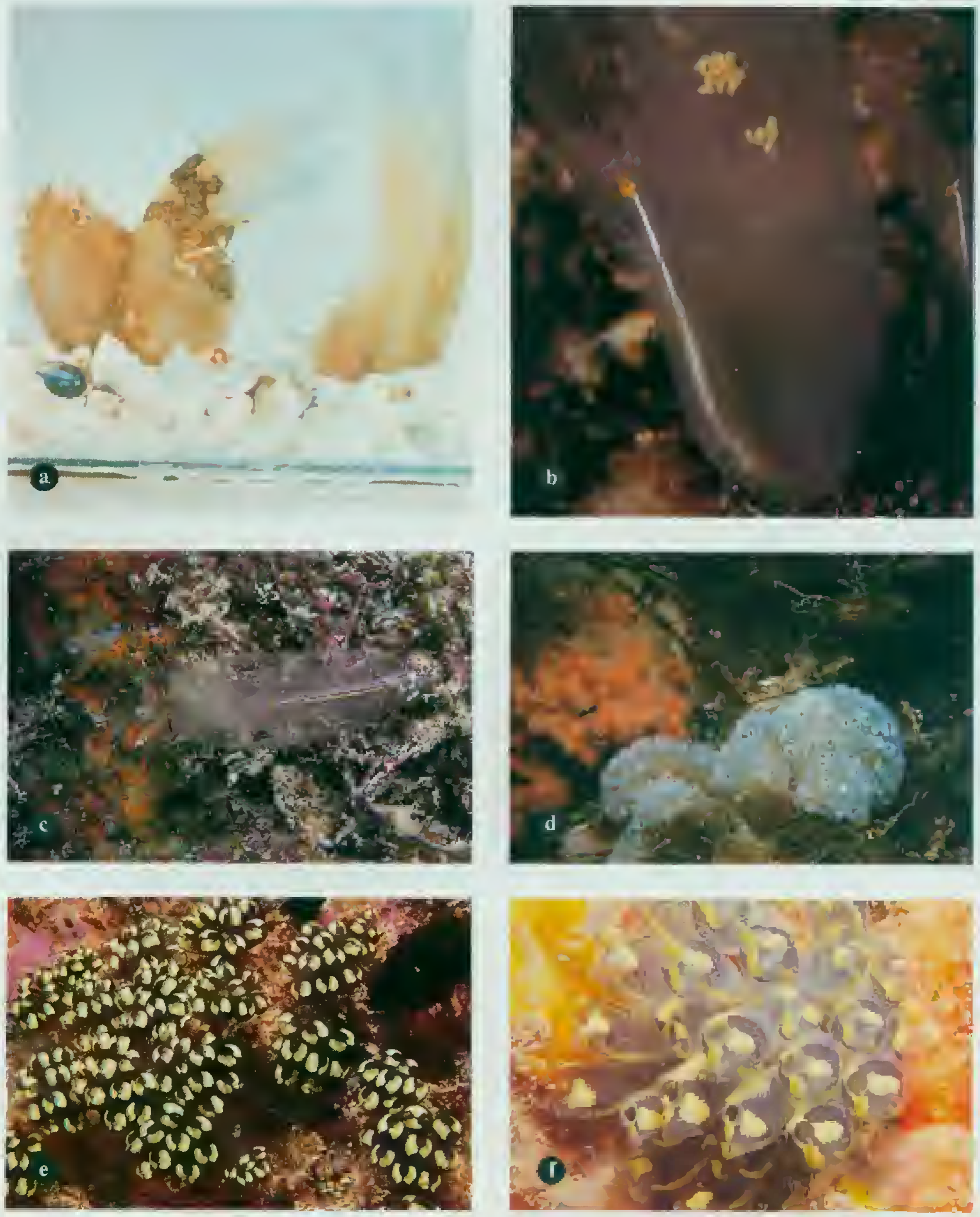


PLATE 1: **a**, *Ciona intestinalis* (Port Phillip Bay, Vic.). **b,c**, *Rhopalaea crassa*, (Heron I., Qld, thoraces only visible, abdomina buried in rubble substrate, rectum, terminating in yellow anus, alongside white vas deferens, yellow ocelli around the border of each aperture, stigmata and muscles clearly seen through the transparent test and body wall — **b**, right side; **c**, dorsum). **d**, *Pseudodiazona claviformis* (SAM E1035 Seacliffe SA). **e,f**, *Clavelina arafurensis* (QM G11988 Exmouth Gulf, WA).

Photos: **a** G. Russ; **b** R. and V. Taylor; **d** N. Holmes; **c,e,f** N. Coleman.

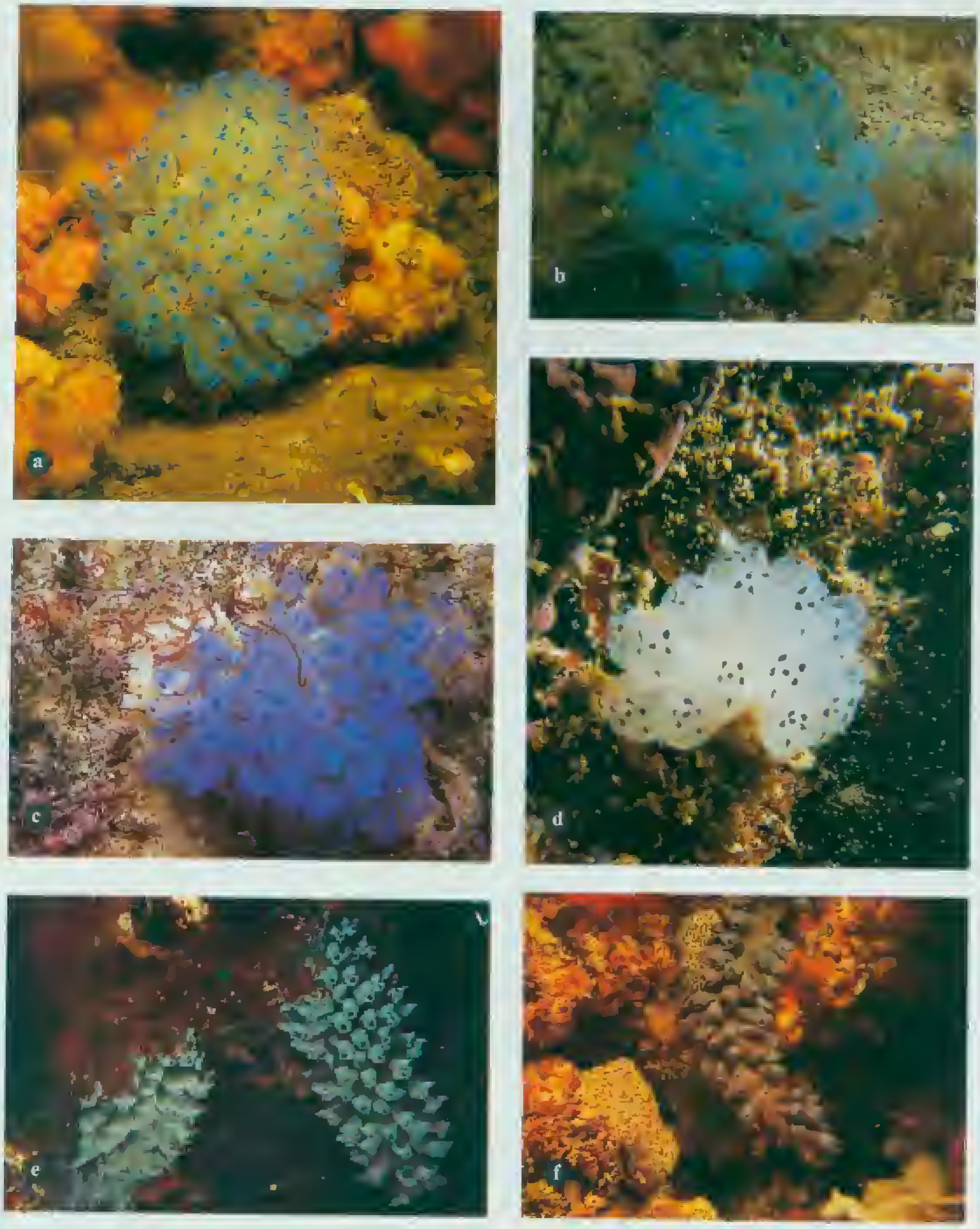


PLATE 2: **a,b,?c,** *Clavelina australis* (**a**, Port Hacking, NSW; **b**, Port Stephens, NSW; **c**, this Great Barrier Reef specimen looks like *C. australis* but the species has not been taken from waters north of Moreton Bay. **d**, *Clavelina baudinensis* (Rottnest I., W.A.). **e,f**, *Clavelina cylindrica* (**e**, QM G9482 Sorrento, WA; **f**, WAM 758.83 Carnac I., WA).

Photos: **a,e,f** N. Coleman; **b** P. Fredrickson; **c** R. and V. Taylor; **d** R. Lethbridge.

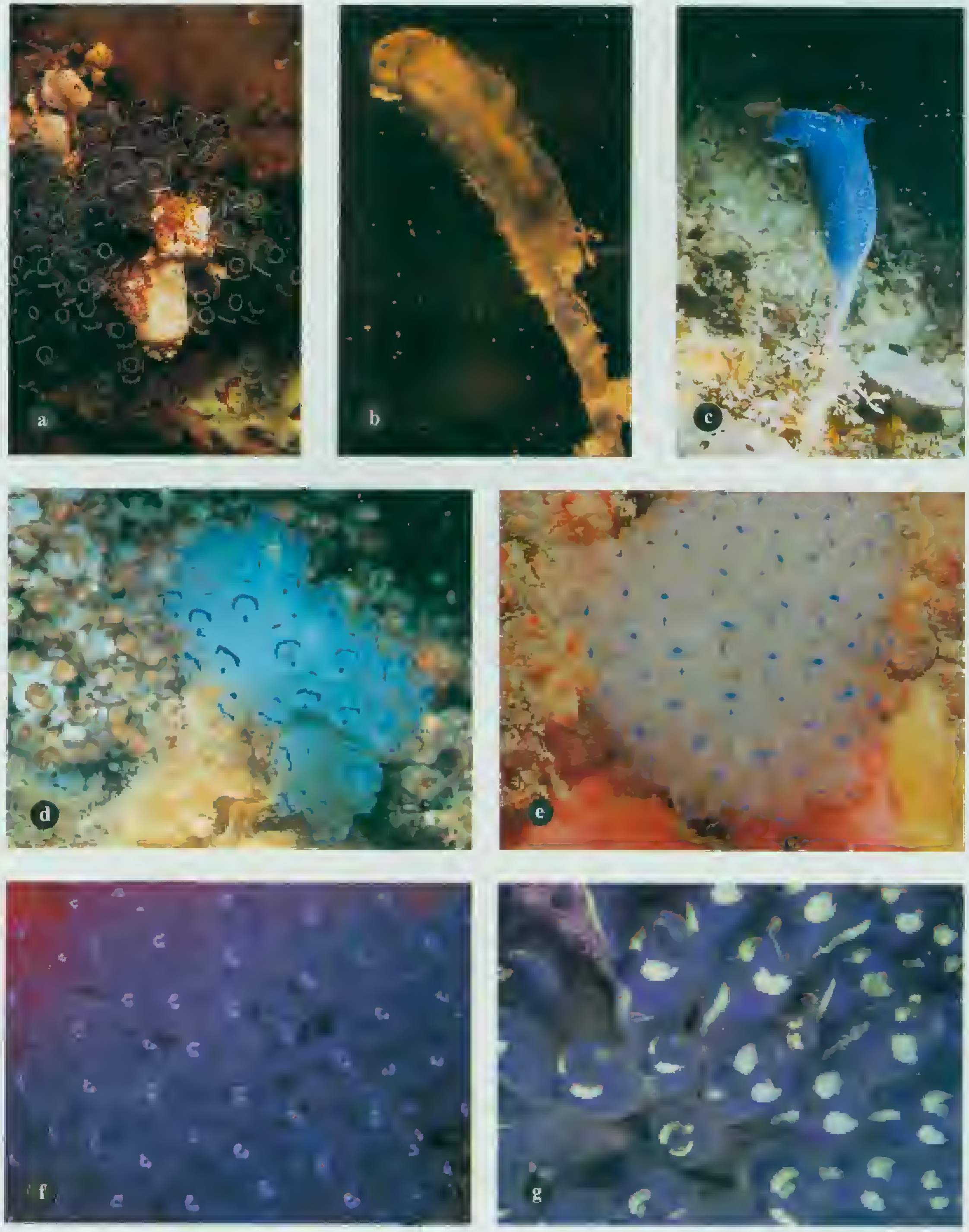


PLATE 4: **a**, *Clavelina nigra* n.sp. (QM G9486 Rottnest I., WA). **b**, *Clavelina oliva* n.sp. (QM GH4108 Lizard I., Qld). **c**, *Clavelina ostrearium* (South Australia). **d,e,?f**, *Clavelina pseudobaudinensis* (showing variations in the extent of pigment patches — **d**, QM G10091 Jervis Bay, NSW; **e**, QM G9484 Portsea, Vic.; **?f**, Lord Howe I.). **g**, ?*Clavelina robusta* n.sp. (Port Hedland, WA).

Photos: **a,e–g** N. Coleman; **b** D. Parry; **c** R. Kuiter; **d** P. Fredrickson.

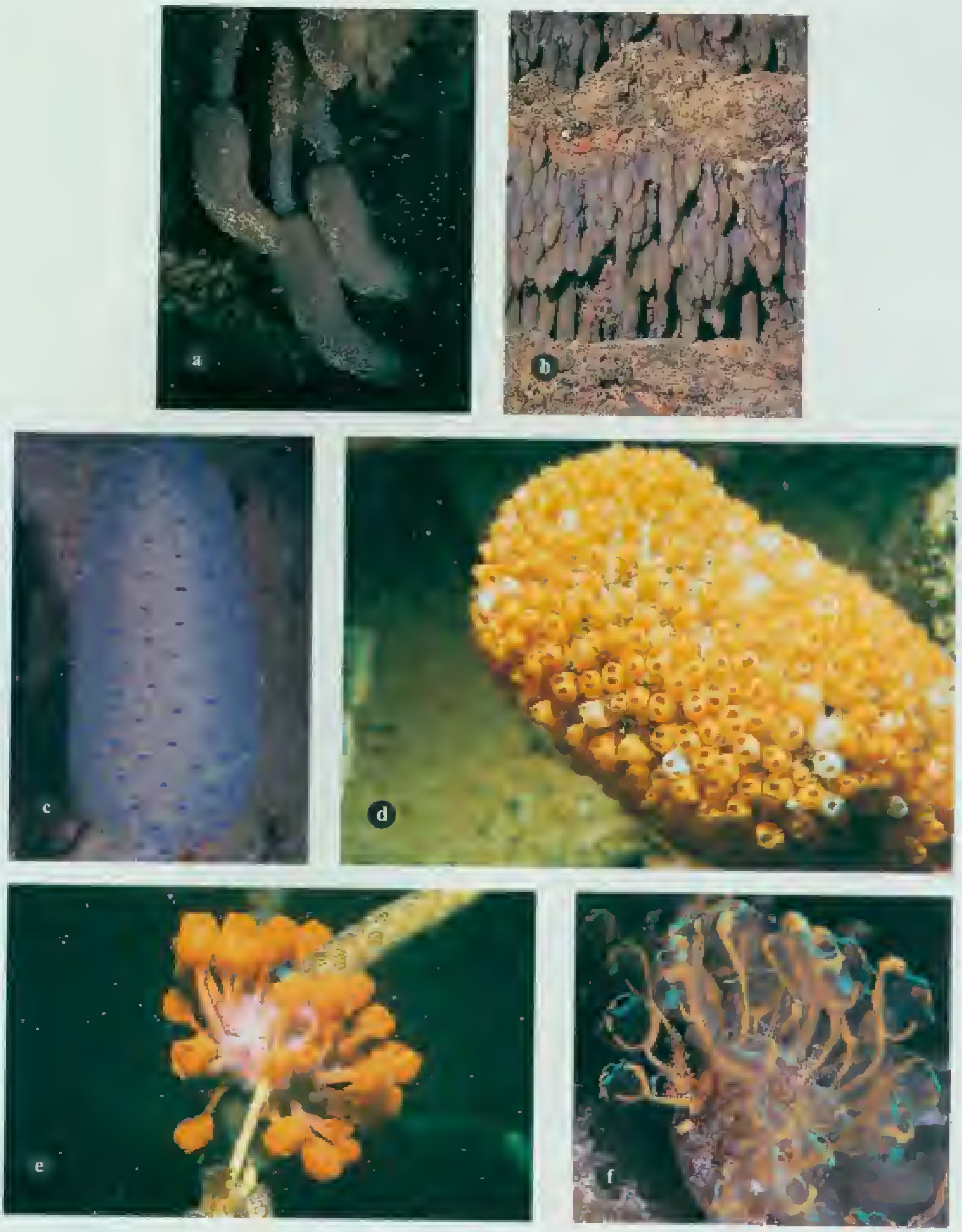


Plate 5: **a–c**, *Nephtheis fascicularis* (**a**, QM GH2093 Martha Ridgeway Reef, Qld; **b**, QM G9258 Roebuck Bay, WA; **c**, Port Hedland, WA). **d**, *Pycnoclavella arenosa* n.sp., (QM GH4360 Erith I., Bass Strait, with yellow thoraces projecting through the white sand on the common stalk). **e**, *Pycnoclavella aurantia* n.sp. (QM GH2295 Nuyts Archipelago, SA). **f**, *Pycnoclavella detorta* (QM G9488 Wistari Reef, Qld).

Photos: **a** E. Lovell; **b,c,e,f** N. Coleman; **d** N. Holmes.

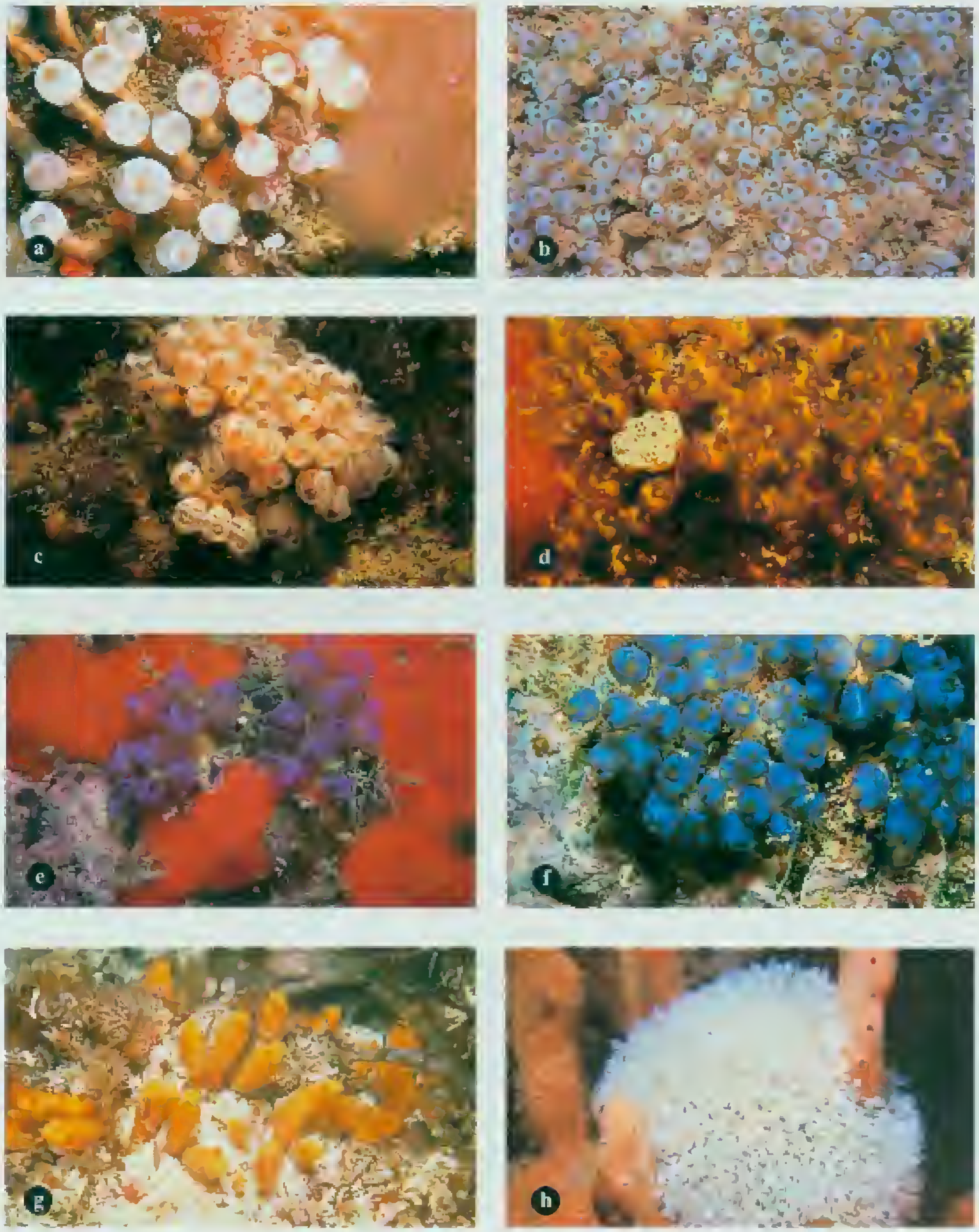


PLATE 6: **a–f**, *Pycnoclavella diminuta* (showing colour variants — **a**, QM GH1302 in caves Ward I., SA; **b**, Port Hedland, WA; **c**, Carnac I., WA; **d**, QM GH4083 Exmouth, W.A.; **e**, Lord Howe I.; **f**, QM G10162 Lizard I., Qld). **g**, *Pycnoclavella elongata* n.sp. (SAM E1981 Franklin I.,-SA). **h**, *Pycnoclavella tabella* n.sp. (Portsea, Vic.).

Photos: **a** R. Kuiter; **b–f,h** N. Coleman; **g** N. Holmes.

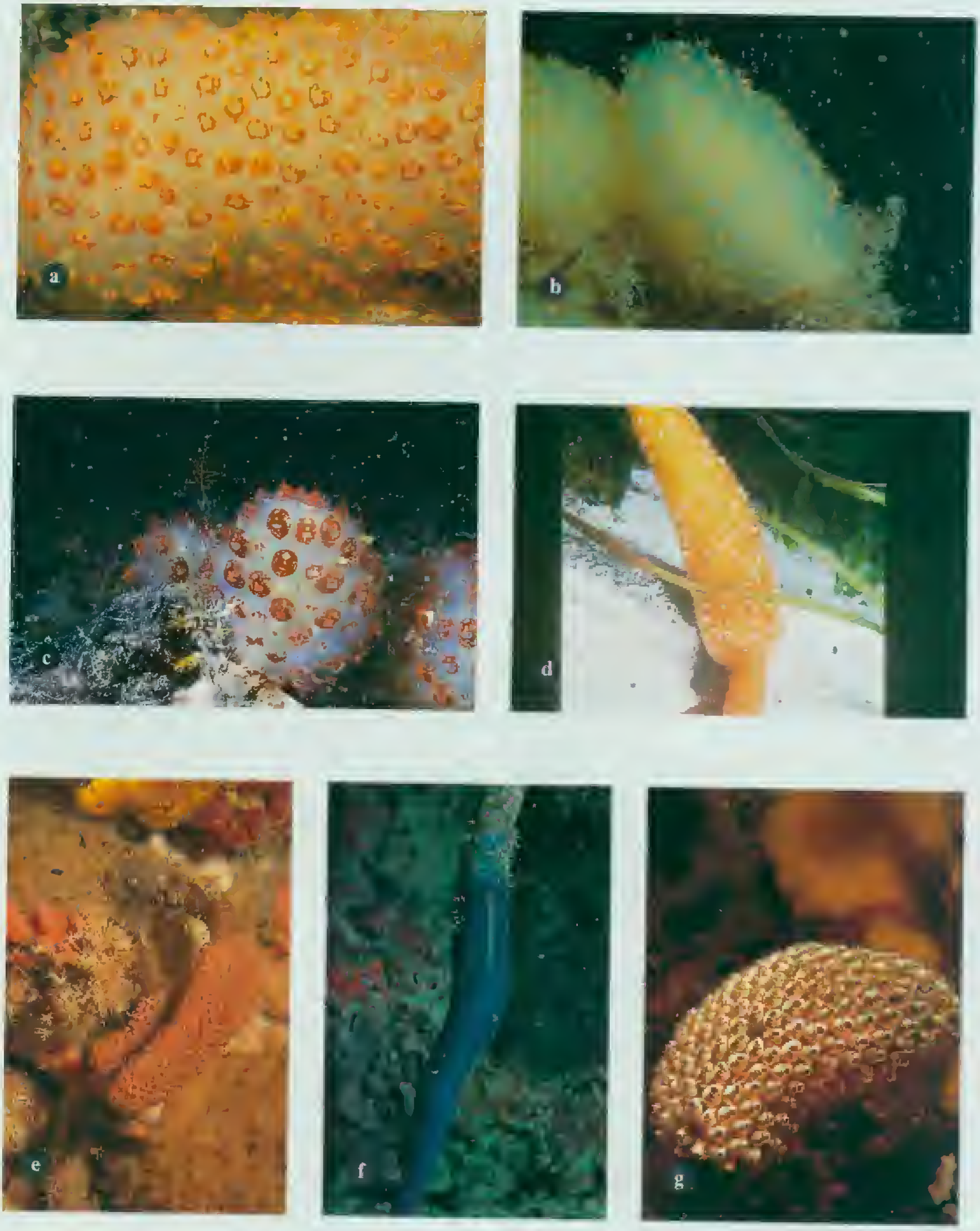


PLATE 7: **a–c**, *Euclavella claviformis* n.gen. (**a**, QM G10152 Port Stephens, NSW; **b**, Port Stephens NSW; **c**, Botany Bay, NSW). **d,e**, *Sigillina australis* (**d**, QM GH944 Great Australian Bight, SA; **e**, Sorrento, WA). **f–g**, *Sigillina cyanea* (**f**, ? NE Qld; **g**, QM G9479 Rottnest I., WA).
Photos: **a,e,g** N. Coleman; **b** P. Fredrickson; **c,d** R. Kuiter; **f** E. Lovell.

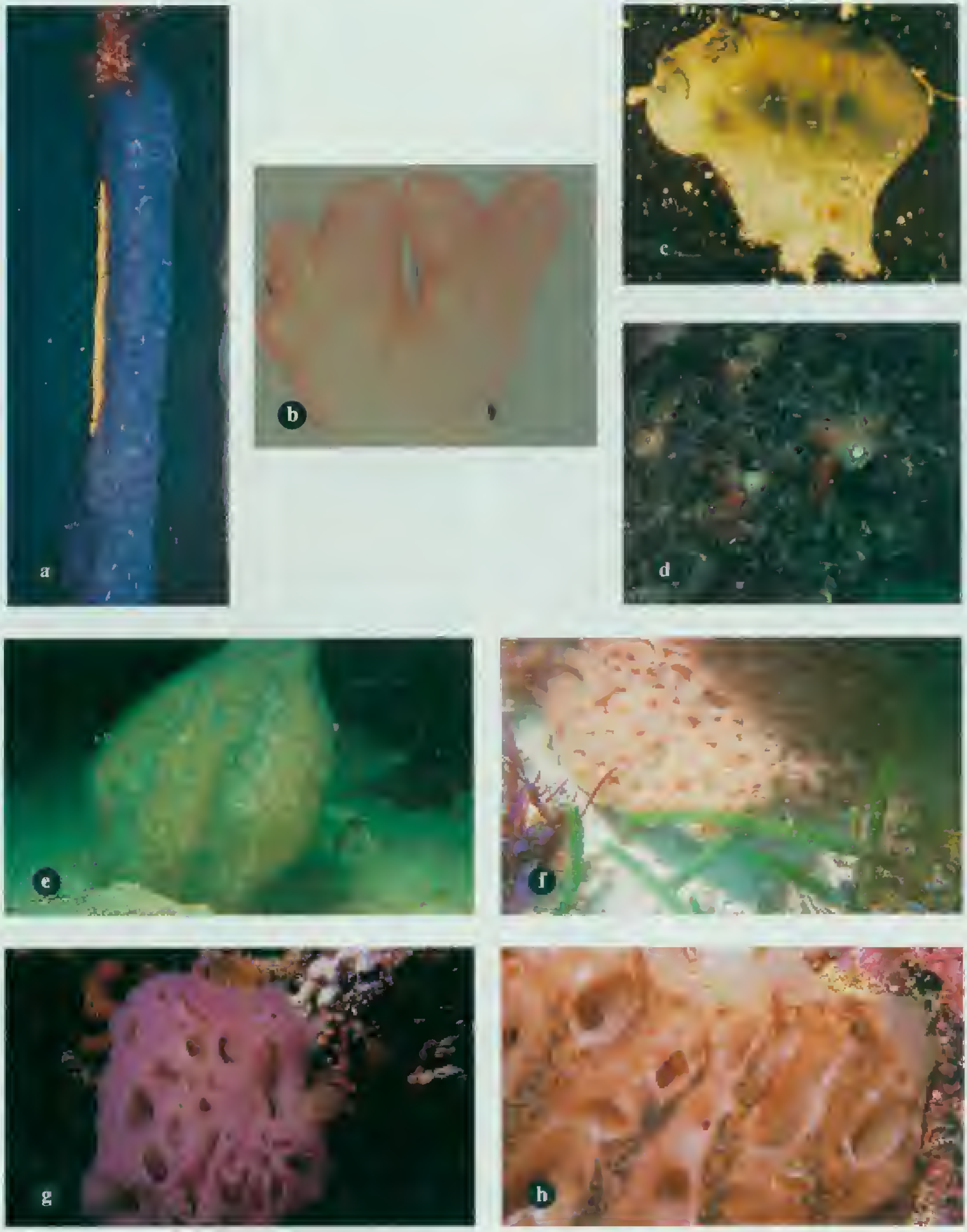


PLATE 8: **a**, *Sigillina fantasiana* (blue colony on *Amphibolus* Spencer Gulf, SA). **b**, *Sigillina grandissima* n.sp. (QM GH1305 Topgallant I., SA). **c,d**, *Sigillina signifera* (**c**, Lizard I., Qld; **d**, QM GH278 Britomart Reef, Qld). **e**, *Hypodistoma deerratum* (QM G10153 Lizard I., Qld). **f–h**, *Hypodistoma mirabile* (**f**, Golden I., SA; **g**, Perforated I., SA; **h**, QM GH2379 Ward I., SA).

Photos: **a,b** S. Shepherd; **c** D. Parry; **d** E. Lovell; **e** N. Coleman; **f,g** W.H. Sasse; **h** N. Holmes.

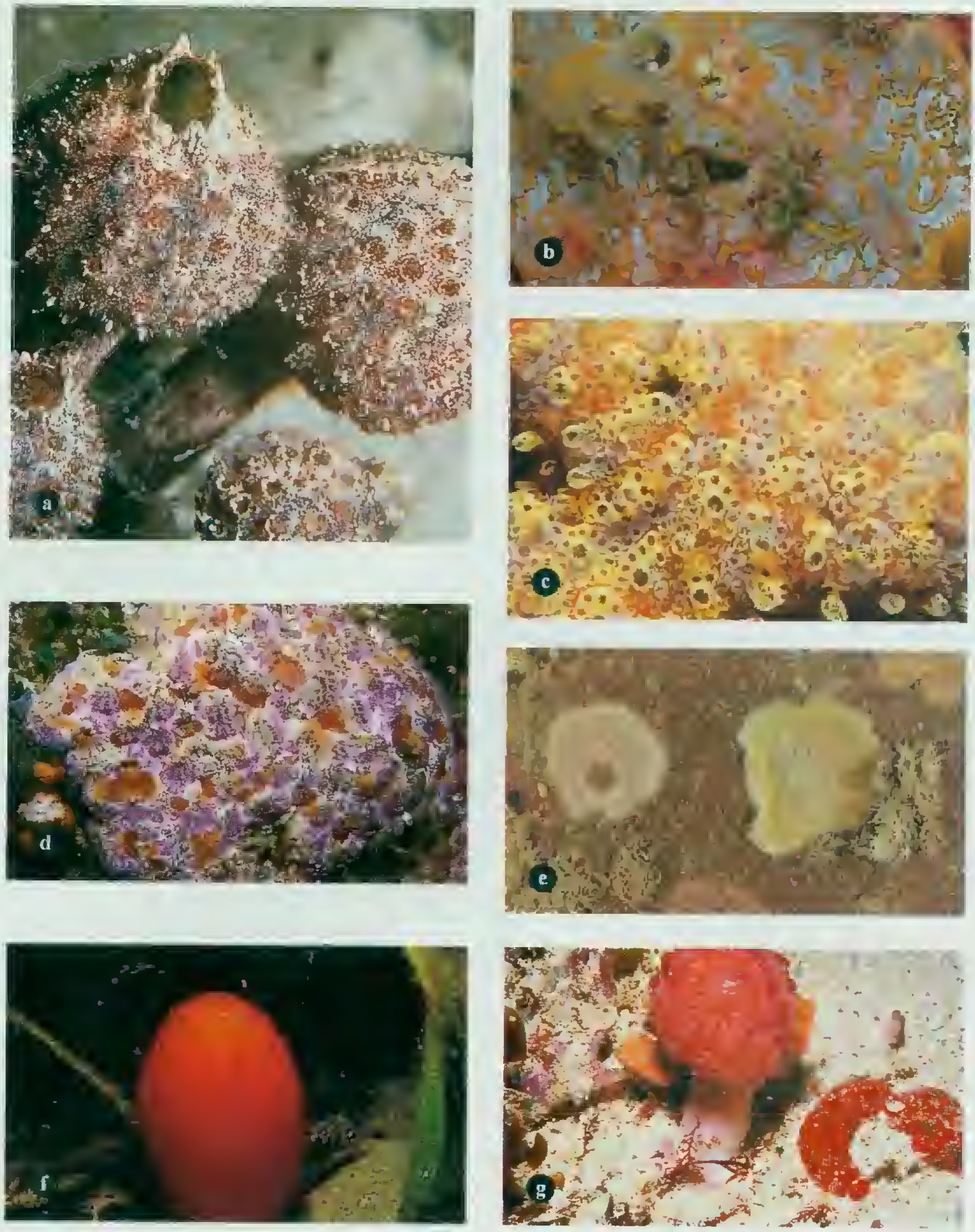


PLATE 9: **a**, *Distaplia australiensis* (South Australia). **b**, *Distaplia dubia* (QM GH52 Lord Howe I.). **c,d**, *Distaplia florida* n.sp. (QM GH4103 Byron Bay, NSW — **c**, colony relaxed; **d**, colony contracted). **e**, *Distaplia pallida* n.sp. (colonies on experimental fouling plate QM G11924 Portsea Pier, Vic.). **f,g**, *Distaplia stylifera* (**f**, Fremantle WA; **g**, QM GH2407 Hotspot, SA).

Photos: **a,g** N. Holmes; **b–d,f** N. Coleman; **e** G. Russ.

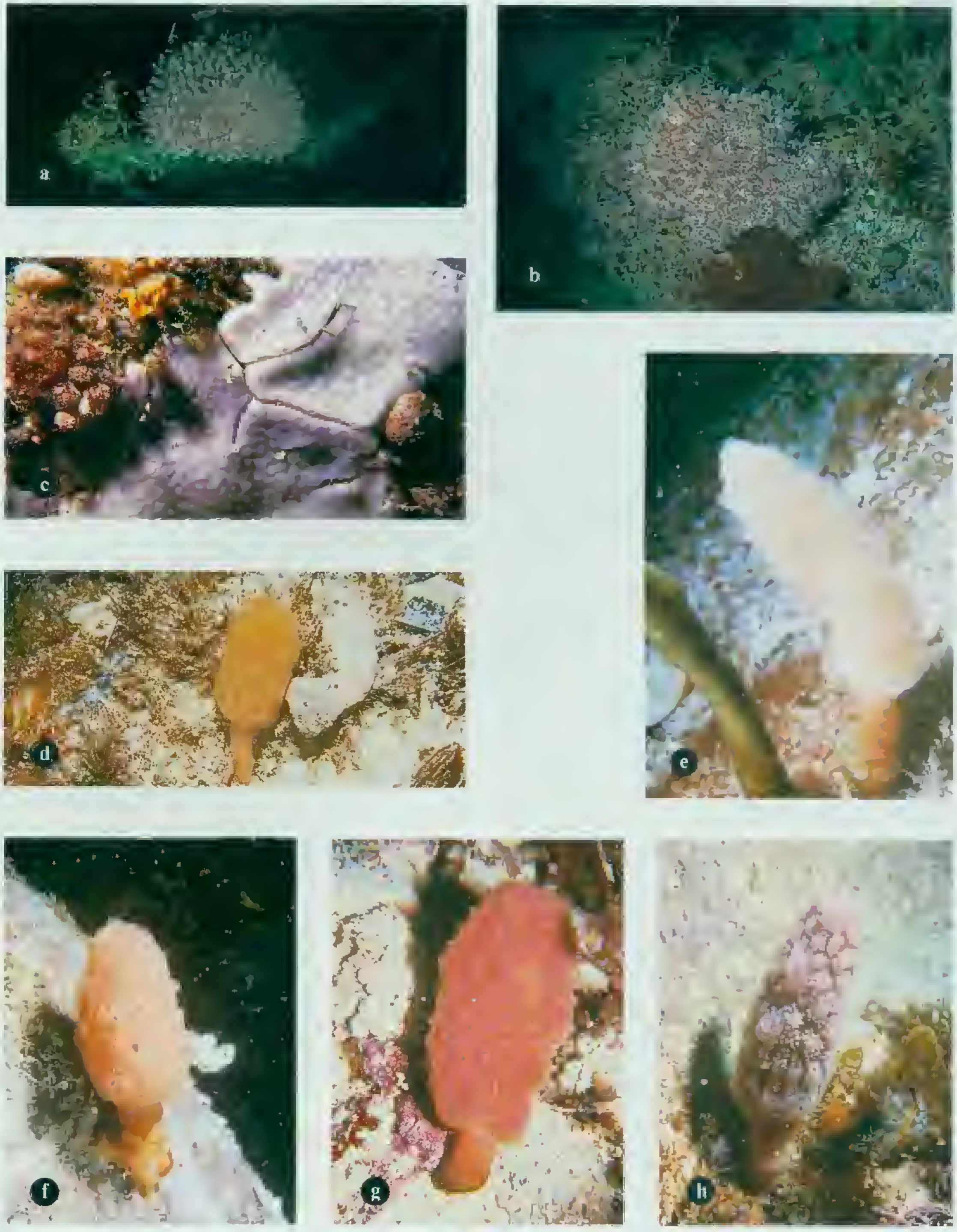


Plate 10: **a–c**, *Distaplia viridis* (**a,b**, QM GH45 Portland, Vic.; **c**, QM GH4159 Golden I., SA). **d–h**, *Hypsistozoa distomoides*, showing colour variants (**d,e**, Flinders I., SA; **f**, QM GH1280 Ward I., SA; **g**, QM GH2390 Hotspot, SA; **h**, QM GH1297 Ward I., SA).
Photos: **a,b** N. Coleman; **c,d,g** N. Holmes; **e,f,h**, R. Kuiter.

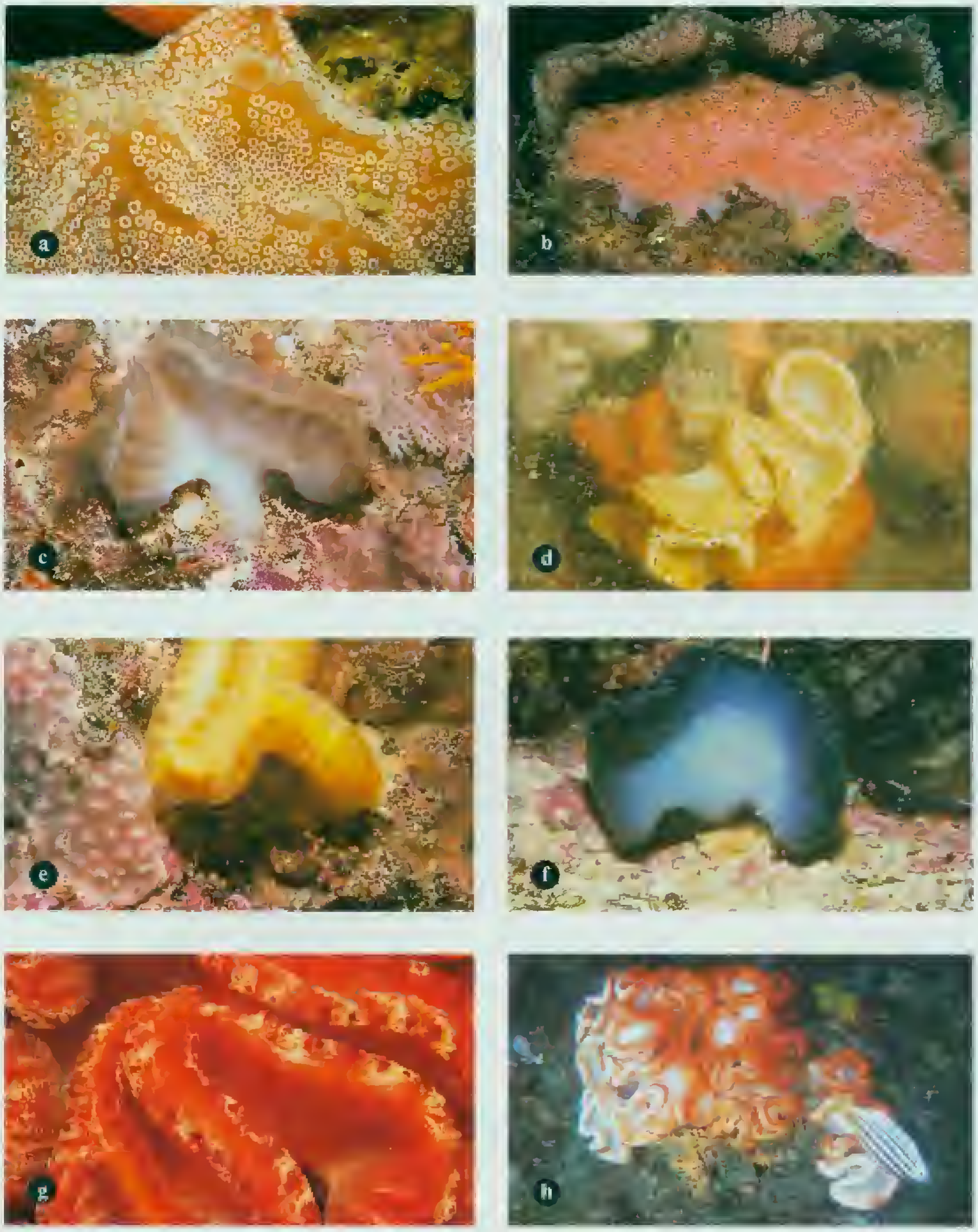


PLATE 11: **a,b**, *Neodistoma mammillatum* n.gen. n.sp. (SAM E1984 Seacliffe, SA). **c–h**, *Sycozoa cerebriformis* (colour variants — **c**, QM GH2394 Flinders I., SA; **d**, Jervis Bay, NSW; **e**, QM GH2393 Flinders I., SA; **f**, QM GH2284 Nuyts Archipelago, SA; **g**, detail of colony Port Hacking, NSW; **h**, well developed colony, South Australia).
Photos: **a–c,e,f** N. Holmes; **d** P. Fredrickson; **g** N. Coleman; **h** R. Kuiter.

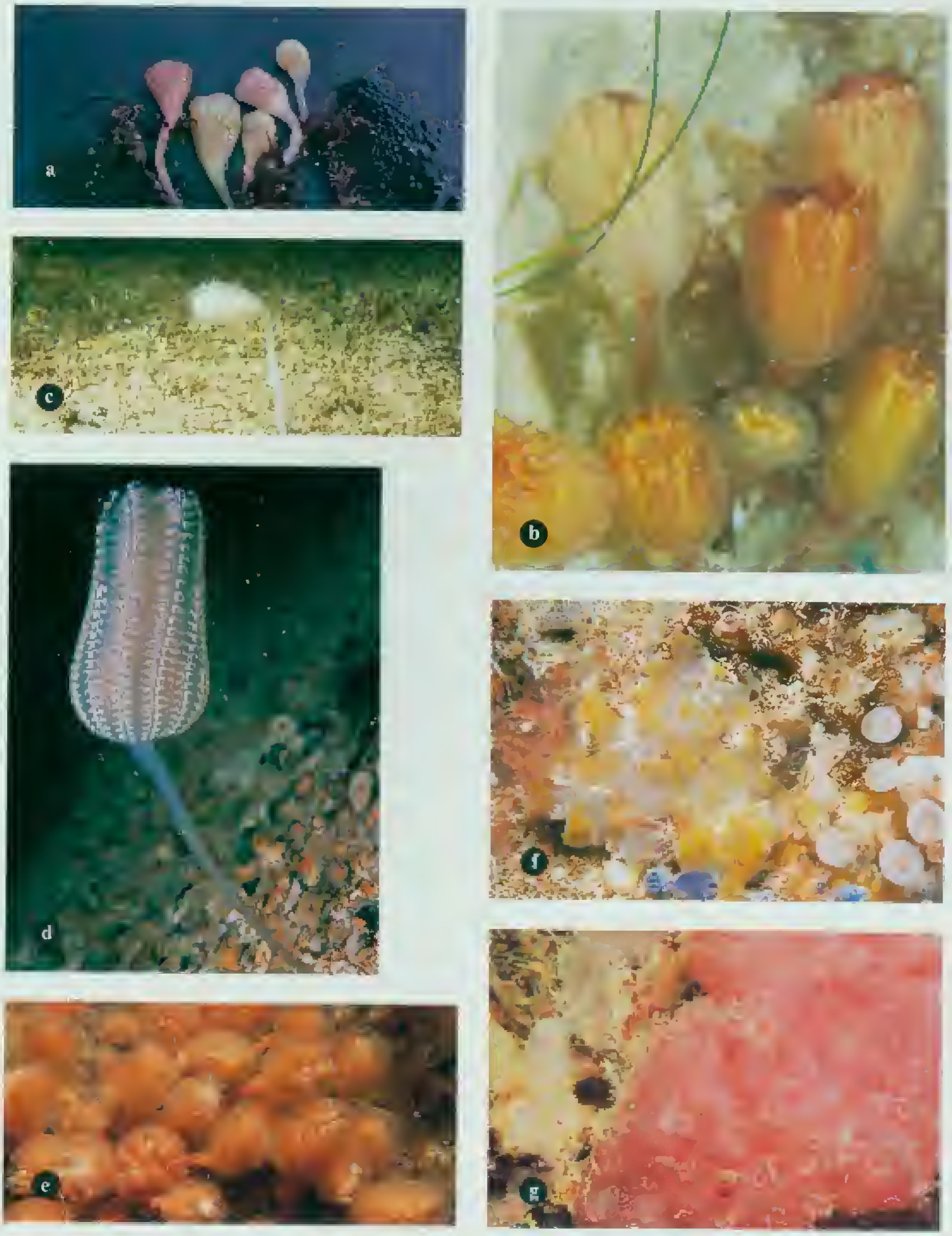


PLATE 12. **a**, *Sycozoa murrayi* (QM GH4155 the Gap, SA). **b**, *Sycozoa pedunculata* (South Australia). **c,d**, *Sycozoa pulchra* (South Australia). **e**, *Sycozoa sigillinoides* (QM G10148 St. Helens, Tas.). **f**, *Stomozoa australiensis* n.sp. (QM GH2392 Ward I., SA). **g**, *Stomozoa bellissima* n.sp. (QM G9267 Exmouth Gulf, WA).
Photos: **a** W.H. Sasse; **b,c** R. Kuiter; **d** N. Holmes; **e,g** N. Coleman; **f** S.A. Shepherd.

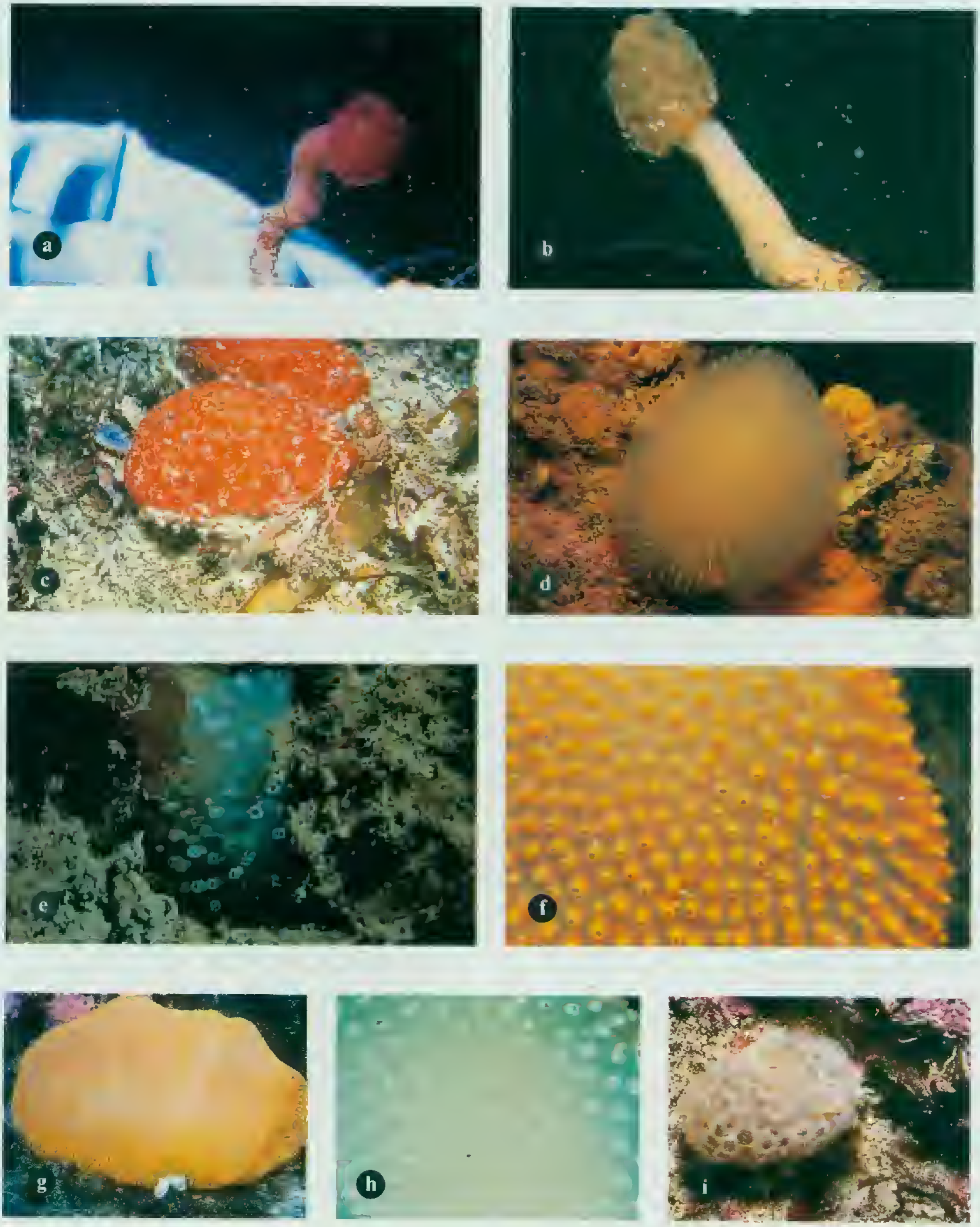


PLATE 13. **a,b**, *Polycitor calamus* n.sp. (**a**, QM GH4188 Avoid Bay, SA; **b**, SAM E2057 Flinders I., SA). **c**, *Polycitor cerasus* n.sp. (SAM E2080 Nuyts Archipelago, SA). **d–h**, *Polycitor giganteus* (**d**, Port Noarlunga, SA; **e**, Port Stephens, NSW; **f**, Bass Strait; **g**, South Australia; **h**, Botany Bay, NSW). **i**, *Polycitor nubilus* n.sp. (SAM E2079 Flinders I., SA).

Photos: **a** W.H. Sasse; **b,c,i** N. Holmes; **d,f,h** N. Coleman; **e** P. Fredrickson; **g** R. Kuiter.

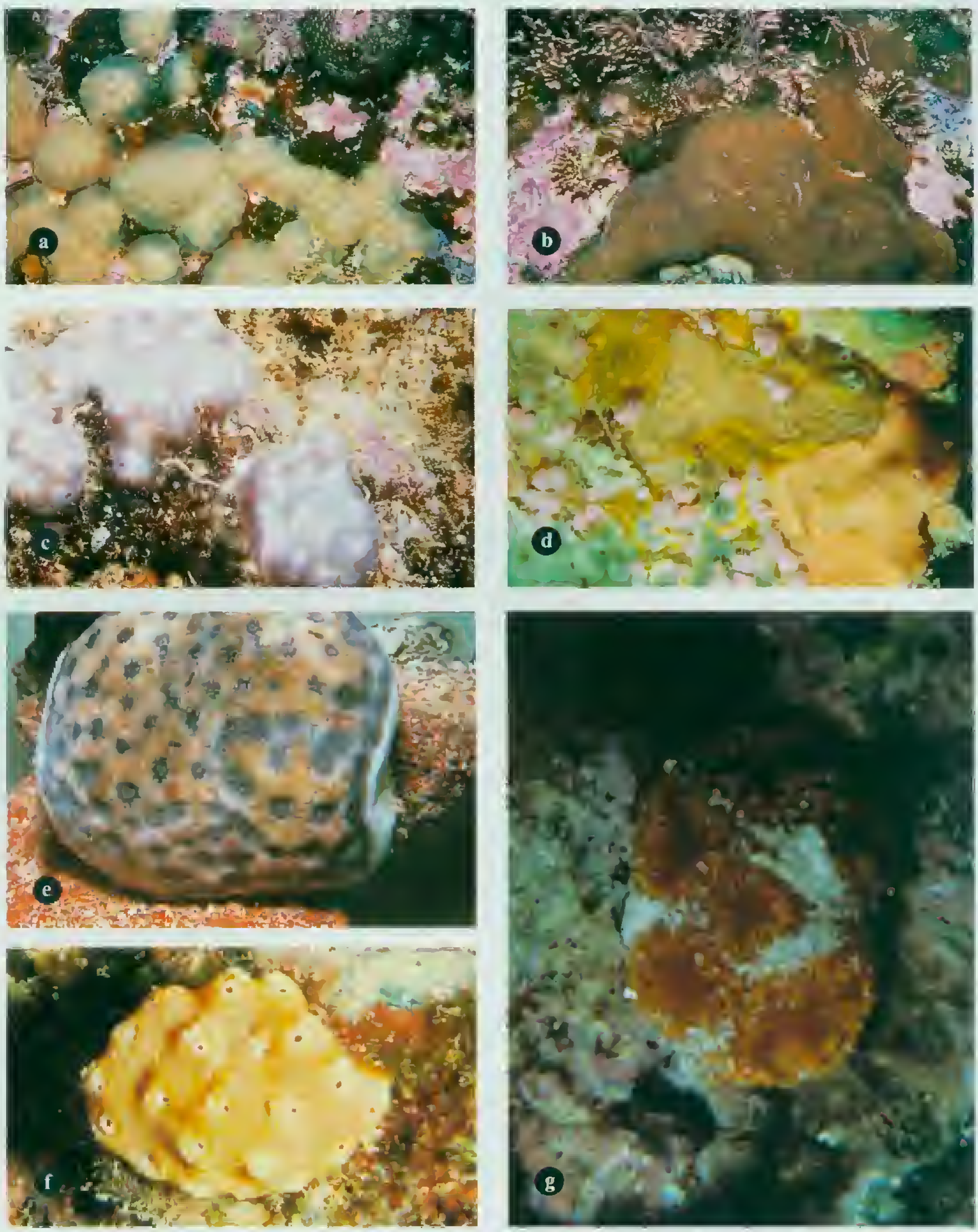


PLATE 14. **a–d**, *Cystodytes dellachiajei* (**a**, QM GH2401 West I., SA; **b**, QM GH2402 West I., SA; **c**, South Australia; **d**, New South Wales). **e**, *Polycitorella coronaria* (QM GH2377 Hotspot, SA). **f,g**, *Polycitorella orientalis* n.sp. (**f**, QM G9477 Swain Reefs, Qld, contracted specimens, with conspicuous rudimentary cloacal cavities opening to the surface; **g**, Heron I., Qld, extended specimens, the branchial openings conspicuous and the atrial apertures in the shaded cloacal depressions in the centre of each system).

Photos: **a,b** S. A. Shepherd; **c** R. Kuiter; **d,g** P. Fredrickson; **e** N. Holmes; **f** N. Coleman.

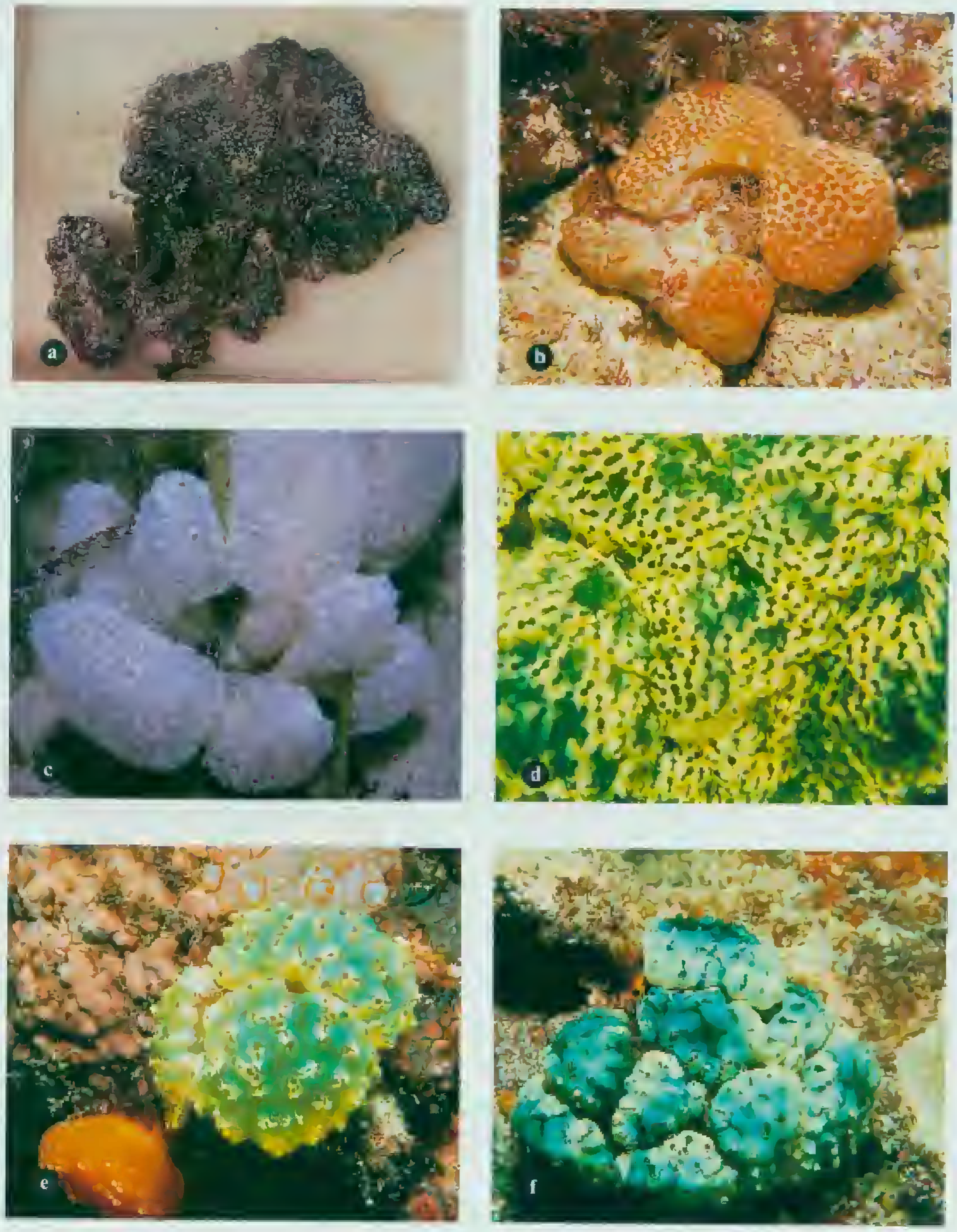


PLATE 15: **a**, *Eudistoma amplum* (Heron I., Qld, with green *Prochloron* on surface). **b**, *Eudistoma constrictum* n.sp. (QM GH2291 Topgallant I., SA). **c**, *Eudistoma elongatum* (Moreton Bay, Qld). **d–f**, *Eudistoma gilboviride* (**d**, crowded lobes, QM G11959 Lizard I., Qld; **e,f**, QM G11961 Swain Reefs, Qld).
Photos: **a** D. Parry; **b** N. Holmes; **c–f** N. Coleman.

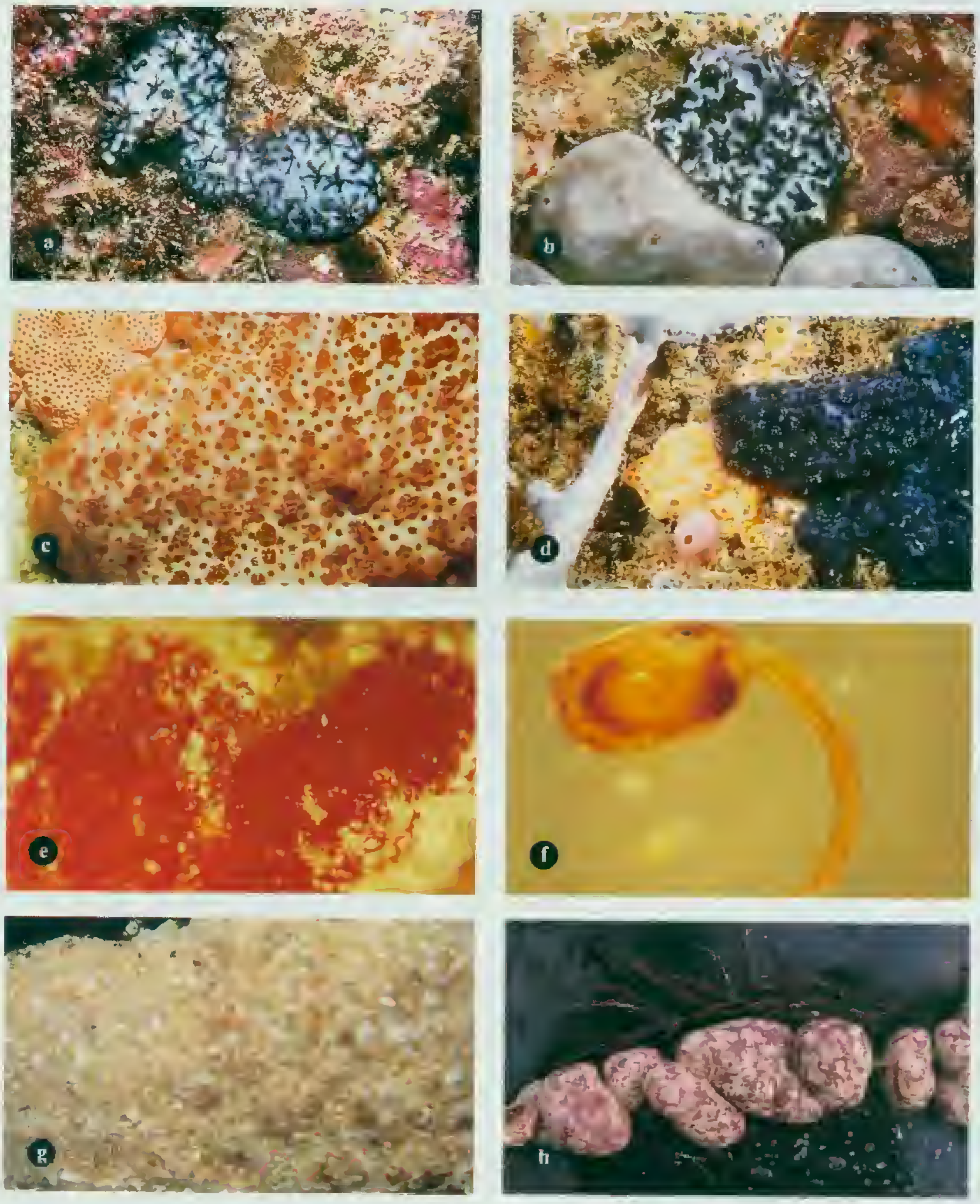


PLATE 16. **a–c,?d**, *Eudistoma maculosum* n.sp. (**a,b**, QM GH2391 Flinders I., SA; **c**, QM GH4605 Jervis Bay, NSW; **d**, ? *E. maculosum* South Australia). **e,f**, *Eudistoma reginum* n.sp. (Heron I., Qld: **e**, colony, depressions representing rudimentary cloacal cavities can be seen as darker shadows in the naked, red areas; **f**, larva, with red pigment accumulated in vicinity of adhesive organs and in the posterior horns of the haemocoelic cavity). **g**, *Eudistoma sabulosum* n.sp. (SAM E2084 Ward I., SA). **h**, *Brevicollus tuberatus* n.gen. n.sp. (SAM E2059 the Gap, SA).

Photos: **a,b** N. Holmes; **c** N. Coleman; **d** R. Kuiter; **e,f** D. Parry; **g** S.A. Shepherd; **h** W.H. Sasse.

LITERATURE CITED

Abbott, D.P. and Trason, W.B. 1968. *Ritterella rubra* and *Distaplia smithi*: two new colonial ascidians from the west coast of North America. *Bull. sth Calif. Acad. Sci.* **67**(3): 143–54.

Agassiz, J.L.R. 1850. On the embryology of *Ascidia* and the characteristics of new species from the shores of Massachusetts. *Proc. Am. Ass.* **1849**: 157–59.

Alder, J. 1863. Observations on the British Tunicata with descriptions of several new species. *Ann. Mag. nat. Hist.* (3)**11**: 153–73.

Alder, J. and Hancock, A. 1907. British Tunicata. II, ed. J. Hopkinson. *Ray Soc. Publs* **2**: 1–164.

Ärnbäck-Christie-Linde, A. 1926. Contributions to the tunicate fauna of Norway, with notes on *Polycitor giganteus* (Sluiter). *Ark. Zool. Stockholm* **18**(1): 1–22.

1927. The genus *Tylobranchion* Herdm. with supplementary notes on *Rhopalaea norvegica* Ärnbäck. *Ark. Zool. Stockholm* **18**(35): 1–20.

1934. Northern and Arctic invertebrates in the collection of the Swedish State Museum. IX Tunicata. Part 4, Agnesiidae, Rhodosomatidae, Ascidiidae, Cionidae. *K. svenska Vetensk-Akad. Handl.* (3)**13**(3): 3–91.

1950. Ascidiacea Part 2, *Further zool. Results Swed. Antarct. Exped.* 1901–1903 **4**(4): 1–41.

Beneden, E. van 1887. Les genres *Ectemascidia* Herd., *Rhopalaea* Phil. et *Sluiteria* n.g. Note pour servir à la classification des Tuniciers. *Bull. Acad. Belg.* (3)**14**(7): 19–44.

Beneden, E. van, and Selys-Longchamps, M. 1913. Tuniciers. Caducichordata (Ascidiaces et Thaliaces). *Résult. Voyage* S.Y. Belgica, *Zoologie*: 1–122.

Berrill, N.J. 1932. Ascidians of the Bermudas. *Biol. Bull. mar. biol. Lab., Woods Hole* **62**: 77–88.

1935a. Studies in tunicate development III. Differential retardation and acceleration. *Phil. Trans. R. Soc.* B **225**: 225–326.

1935b. Studies in tunicate development IV. Asexual reproduction. *Phil. Trans. R. Soc.* B **225**: 327–79.

1936. Studies in tunicate development V. The evolution and classification of ascidians. *Phil. Trans. R. Soc.* B **226**: 43–70.

1947a. The structure, tadpole and budding of the ascidian *Pycnoclavella aurilucens* Garstang. *J. mar. biol. Ass. U.K.* **27**(1): 245–51.

1947b. The structure, development and budding of the ascidian *Eudistoma*. *J. Morph.* **81**: 269–81.

1948a. Tadpole larvae of the ascidians *Polycitor*, *Euherdmania* and *Polysyncraton*. *J. Morph.* **82**: 355–64.

1948b. Budding and the reproductive cycle of *Distaplia*. *Q.J. microsc. Sci.* **89**: 253–89.

1950. The Tunicata. *Ray Soc. Publs* **133**: 1–354.

1955. 'The Origin of Vertebrates' (Oxford University Press: London) 257pp.

Berrill, N.J. and Abbott, D.P. 1949. The structure of the ascidian *Pycnoclavella stanleyi* n.sp. and the nature of its tadpole larva. *Can. J. Res.* **27**: 43–9.

Binney, W.G. 1870. Mollusca. *In* Gould, A.A., 'Report on the Invertebrata of Massachusetts' 2nd. edition, p. 1–27 (Massachusetts Legislature: Boston).

Bonnevie, K. 1896. Ascidiae simplices og Ascidiae compositae. In *Den Norske Nordhavs-Expedition 1876–78* (Christianaia) 23 Zoologie (Tunicata 2): i–iv, 1–16.

Brewin, B.I. 1948. Ascidians of the Hauraki Gulf, Part 1. *Trans. R. Soc. N.Z.* **77**(1): 115–38.

1950. Ascidians of New Zealand, Part 4 — Ascidians in the vicinity of Christchurch. *Trans. R. Soc. N.Z.* **78**(2–3): 344–53.

1951. Ascidians of New Zealand, Part 6 — Ascidians of the Hauraki Gulf, Part 2. *Trans. R. Soc. N.Z.* **79**(1): 104–13.

1952a. Ascidians of New Zealand, Part 7 — Ascidians from Otago coastal waters, Part 2. *Trans. R. Soc. N.Z.* **79**(3–4): 452–8.

1952b. Ascidians of New Zealand, Part 8 — Ascidians of the East Cape region. *Trans. R. Soc. N.Z.* **80**(2): 187–95.

1953. Australian ascidians of the sub-family Holozoinae and a review of the sub-family. *Trans. R. Soc. N.Z.* **81**(1): 53–64.

1956a. *Atapozoa marshi*, a compound ascidian from Western Australia. *J. Proc. R. Soc. West. Aust.* **40**(1): 31–2.

1956b. The growth and development of a viviparous compound ascidian, *Hypsistozoa fasmeriana*. *Q.J. microsc. Sci.* **97**: 435–54.

1956c. Ascidians from the Chatham Is. and the Chatham Rise. *Trans. R. Soc. N.Z.* **84**(1): 121–37.

1958. Ascidians of New Zealand, Part 11 — Ascidians of the Stewart Island region. *Trans. R. Soc. N.Z.* **85**(3): 439–53.

1959. An account of larval budding in the compound ascidian *Hypsistozoa fasmeriana*. *Q.J. microsc. Sci.* **100**(4): 575–89.

1960. Ascidians of New Zealand, Part 13 — Ascidians of the Cook Strait region. *Trans. R. Soc. N.Z.* **88**(1): 119–20.

Brien, P. 1948. Embranchement des tuniciers. In Grassé, P.-P. (ed.) 'Traité de Zoologie' vol. **11**(c) p. 553–751 (Masson et Cie: Paris).

Bronn, H.G. 1862. Weichthiere. *In* 'Die Klassen und Ordnungen des ThierReichs' vol. 3(1) p. 103–223 (C.F. Winter: Leipzig).

Castle, W.E. 1896. The early embryology of *Ciona intestinalis* Fleming (L.). *Bull. Mus. comp. Zool. Harv.* 27(7): 203–80.

Caullery, M. 1895. Sur l'anatomie et la position systématique du genre *Sigillina*. *C.r. hebd. Séanc. Acad. Sci. Paris* **121**: 832–4.

1900. Sur des clavelines nouvelles (*Synclavella*), réalisant de cormus d'ascidies composées. *C.r. hebd. Séanc. Acad. Sci. Paris* 13. 1418–20.

1908. Sur une forme de tuniciers provenant de l'expédition de *l'Astrolabe* (1829) et le genre *Chondrostachys* Macdonald. *Bull. Mus. natn. Hist. nat. Paris* 14: 229–32.

1909. Récherches sur la famille des Distomidae. *Bull. scient. Fr. Belg.* **42**: 1–59.

Cloney, R.A. 1977. Larval adhesive organs and metamorphosis in ascidians I. Fine structure of the everting papillae of *Distaplia occidentalis*. *Cell. Tiss. Res.* **183**: 423-44.

Couthouy, J.T. 1838. Descriptions of new species of Mollusca and shells. *J. nat. Hist. Boston* **2**: 53-111.

Cunningham, R.O. 1871. Notes on the reptiles, amphibia, fishes, Mollusca and Crustacea obtained during the voyage of *H.M.S. Nassau* in the years 1866-1869. *Trans. Linn. Soc. Lond.* **27**: 465-502.

Cuvier, G. 1815. Mémoire sur les ascidies et sur leur anatomique. *Mém. Mus. natn. Hist. nat. Paris* **2**: 10-39.

Dall, W.H. 1870. Revision of the classification of the Mollusca of Massachusetts. *Proc. Boston Soc. nat. Hist.* **13**: 240-57.

Damas, D. 1899. Les formations epicardiques chez *Ciona intestinalis*. *Archs Biol. Paris* **16**: 1-25.

Dekay, J.E. 1843. Part 5. Mollusca. *In* 'Natural History of New York' p. 258-60 (New York Assembly: Albany) vii,271 pp.

Della valle, A. 1877. 'Contribuzioni alla storia naturalle delle ascidie composte del Golfo di Napoli con la descrizione di alcune specie e varieta nuove di altre poconate' (Napoli): (*fide* Seeliger, O., 1893).

1881. Nouvi contribuzioni alla storia naturalle delle ascidie composte del Golfo di Napoli. *Atti Accad. nag. Lincei Series 3. Memoir.* **10**(3): 431-98.

Delle Chiaje, S. 1841. 'Descrizione e Notomia degli Animali Invertebrati della Sicilia osservati negli anni 1822-30' vol. 3 p. 13-46 (Napoli).

Drasche, R. von 1882. *Oxycorinia*, eine neue Synascidien-Gattung. *Verh. zool.-bot. Ges. Wien* **32**: 175-8.

1883. Die Synascidien der Bucht von Rovigno (Istrien). *In* 'Ein Beitrag zur Fauna der Adria' (Wien) 41 pp.

1884. Ueber einige neue und weniger gekannte aussereuropäische einfache Ascidien. *Denkschr. Akad. Wiss., Wien.* **48**: 369-87.

Fleming, J. 1822. 'The Philosophy of Zoology' vol. 2, pp. 508-18 (Edinburgh and London).

Forbes, E., and Hanley, S.C.T. 1848. 'A history of British Molluscs and their shells' vol. 1 (London).

Frederickson, P. 1978. 'Metals in the marine environment' MSc. thesis (Macquarie University: Sydney).

Gaertner, J. 1774. Zoophyta, quaedam minuta. *In* Pallas, P.S. (ed.), 'Specilegia Zoologia' *fasc.* **10**. p. 24-41 (G.A. Lange: Berolini).

Garstang, W. 1891. Note on a new and primitive type of compound ascidian. *Ann. Mag. nat. Hist.* (6)**8**: 265-8.

Giard, A.M. 1872. Récherches sur les ascidies composées ou synascidies. *Archs Zool. exp. gén.* **1**: 501-704.

Goodbody, I. 1974. The physiology of ascidians. *Adv. mar. Biol.* **12**: 1-129.

Gould, A.A. 1856. Mollusca and shells. *United States exploring expedition during the years 1838-1842 under the command of Charles Wilkes*, Atlas; 1-16, pls 1-56.

Gunnerus, J.E. 1765. Söe-Püngen (Tethyum sociabile) fuldständige beskreven. *Trondhj. Selsk. Skrift.* **3**: 81-102. (Translated 1767; Vollständige Beschreibung des Seebeutels. *Drontheim. Gesellsch. Schrift.* **3**: 69).

Hancock, A. 1870. On the larval state of *Molgula* with a description of several new species of simple ascidians. *Ann. Mag. nat. Hist.* (4)**6**: 353-68.

Harant, H. 1925. Ascidies récoltées au cours des compagnes scientifiques de S.A.S. le Prince Albert Ier de Monaco (note préliminaire). *Bull. Inst. océanogr. Monaco* **467**: 1-6.

1929. Ascidies provenant des croisières du Prince Albert Ier de Monaco. *Résultats de Campagnes Scientific accomplies sur son Yacht par Albert Ier (Monaco)* **75**: 1-110.

Harant, H. and Vernières, P. 1938. Ascidiae compositae. *Scient. Rep. Australas. Antarct. Exped. 1911-14* **3**(5): 1-13.

Hartmeyer, R. 1899. Die monascidien der Bremer expedition nach Ostspitzbergen. *Zool. Jahrb. Syst.* **12**: 453-511.

1903. Die Ascidien der Arktis. *Fauna arct.* **3**(2): 93-412.

1905. Ascidiens von Mauritius. *Zool. Jb.* **8**: 383-406.

1909. Ascidien (continuation of work by Seeliger). *In* Bronn, H.G. (ed.) 'Klassen und Ordnungen des Tierreichs' vol. 3, suppl. (89-98); p. 1281-772 (C.F. Winter: Leipzig). Abstract, repeating lists of species by Schepotieff, A. 1911, in *Arch. Naturgesch.* **6**: 3-27.

1911. Die Ascidien der Deutschen Südpolar-Expedition 1901-1903. *Dt. Südpol-Exped. (1905-31)* **12**(4): 407-606.

1912. Die Ascidien der Deutschen Tiefsee Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped.* Valdivia' **16**(3): 223-392.

1915a. Alder und Hancock's Britische Tunicaten. Eine Revision. *Mitt. zool. Mus. Berl.* **7**: 303-44.

1915b. Ascidian nomina conservanda. *Sber. Ges. naturf. Freunde Berl.* **1915**: 247-58.

1919. Ascidien. *In* Results of Dr E. Mjöberg's Swedish scientific expeditions to Australia 1910-13. *K. svenska Vetensk-Akad.* **60**(4): 1-150.

1920. Mitteilung. *In* Kukenthal, W. (ed.) 'Die Bedeutung der Verbreitung mariner Bodentiere für die Palaogeographie'. *Sber. Ges. naturf. Freunde Berl.* **1919**: 210, 305.

1922. Die ascidienfauna des Trondhjemfjords. Meddelese fra Trondhjems Biologiske Station 14. *K. norske Vidensk. Selsk. Skr.* **1921**(6): 1-47.

1924. Ascidiacea, part II. Zugleich eine übersicht über die arktische und boreale Ascidienfauna auf tiergeographischer Grundlage. *Ingolf-Exped.* **2**(7): 1-275.

Hartmeyer, R., and Michaelsen, W. 1928. Ascidiae Diktyobranchiae und Ptychobranchiae. *Fauna Südwest-Aust.* **5**: 251-460.

Hastings, A.B. 1931. Tunicata. *Scient. Rep. Gt Barrier Reef Exped.* **4**(3): 69-109.

Hawkins, C.J., Kott, P., Parry, D.L. and Swinehart, J.H. 1983. Vanadium content and oxidation state related to ascidian phylogeny. *Comp. Biochem. Physiol.* **76**B(3): 555–8.

HELLER, C. 1875. Untersuchungen über die Tunicaten des Adriatischen Meeres (2). *Denkschr. Akad. wiss. Wien* **36**, 107–25.

HERDMAN, W.A. 1880. Preliminary report on the Tunicata of the Challenger expedition. Ascidiidae. *Proc. R. Soc. Edinb.* **10**(1): 458–72.

1882. Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Pt. I, Ascidiae simplices. *Zool. Chall. Exp.* **6**(17): 1–296.

1886. Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Pt. II, Ascidiae compositae. *Zool. Chall. Exp.* **14**(38): 1–425.

1890. On the genus *Ecteinascidia* and its relations; with descriptions of two new species, and a classification of the family Clavelinidae. *Proc. Trans. Lpool biol. Soc.* **5**: 144–63.

1891. A revised classification of the Tunicata, with definitions of the orders, sub-orders, families, subfamilies and genera, and analytical keys to the species. *J. Linn. Soc. Lond. Zool.* **23**: 558–652.

1899. Descriptive catalogue of the Tunicata in the Australian Museum. *Australian Museum, Sydney, Catalogue* **17**: 1–139.

1906. Report on the Tunicata. *Ceylon Pearl Oyster Fisheries* suppl. rept. **39**: 295-348.

HERDMAN, W.A. AND RIDDELL, W. 1913. The Tunicata of the *Thetis* Expedition. *In* 'Scientific results of the Trawl Expedition *Thetis*' Part 17. *Mem. Aust. Mus.* **4**: 873–89.

HIRSCHLER, A. 1914. Ueber die Restitutions und Involutions-vorgänge bei operierten Examplaren von *Ciona intestinalis* Flem. *Arch. Mikrosk. Anat. EntwMech.* **85**: 205-27.

HOSHINO, Z. AND NISHIKAWA, T. 1985. Taxonomic studies of *Ciona intestinalis* (L.) and its allies. *Publs Seto mar. biol. Lab.* **30**(1–3): 61–79.

HOSHINO, Z. AND TOKIOKA, T. 1967. An unusually robust *Ciona* from the northeastern coast of Honsyu Island, Japan. *Publs Seto mar. biol. Lab.* **15**(4): 275–90.

HUNTSMAN, A.G. 1912a. Holosomatous ascidians from the coast of western Canada. *Contr. Can. Biol. Fish.* 1906–1910: 103–85.

1912b. Ascidians from the coasts of Canada. *Trans. R. Can. Inst.* **9**: 111–48.

HUUS, J. 1937. Ascidiaceae Tethyodeae Seescheiden. *In* Kukenthal, W. and Krumbach, T. (eds) *Handb. Zool.* **5**(2)6: 545-672.

JULIN, C. 1904. Recherches sur la phylogenèse des tuniciers *Archiascidia neapolitana* nov. gen. *Mitt. zool. Stn Neapel* **16**: 489–552.

KESTEVEN, H.L. 1909. Studies on Tunicata no. 1. *Proc. Linn. Soc. N.S.W.* **34**: 276-95.

KINGSLEY, J.S. 1901. Preliminary catalogue of the marine invertebrates of Casco Bay, Maine. *Proc. Portland Soc. nat. Hist.* **2**: 159–83.

KOTT, P. 1952. Ascidians of Australia. I. Stolidobranchiata and Phlebobranchiata. *Aust. J. mar. Freshw. Res.* **3**(3): 206–333.

1954. Tunicata. *Rep. B.A.N.Z. antarct. Res. Exped.* **1**(4): 121-82.

1957a. Ascidians of Australia II. Aplousobranchiata Lahille; Clavelinidae Forbes and Hanley and Polyclinidae Verrill. *Aust. J. mar. Freshw. Res.* **8**(1): 64–110.

1957b. The sessile Tunicata. *Scient. Rep. John Murray Exped.* **10**(4): 129–50.

1957c. Some tunicates from Macquarie Island and Heard Island. *A.N.A.R.E. Rep.* (Ser. B) **1**: 1–4.

1962. The ascidians of Australia III. Aplousobranchiata Lahille: Didemnidae Giard. *Aust. J. mar. Freshw. Res* **13**(3): 265–334.

1963. The ascidians of Australia IV. Aplousobranchiata Lahille; Polyclinidae Verrill (continued). *Aust. J. mar. Freshw. Res.* **14**(1): 70–118.

1966. Ascidians of northern Australia. *Pap. Dep. Zool. Univ. Qd* **2**(15): 279–304.

1967. *Atopozoa deerata* (Sluiter); a discussion of the relationships of the genus and species. *Proc. Linn. Soc. N.S.W.* **91**(3): 185–8.

1969. Antarctic Ascidiacea. A monographic account of the known species based on specimens collected under U.S. Government auspices 1947 to 1963. *Antarct. Res. Ser.* **13**: i–xv, 1–239.

1971. Antarctic Ascidacea II. Collections made south of 40 south latitude 1963/67, principally by the U.S.N.S. *Eltanin*. *Antarct. Res. Ser.* Biology **16**(4): i–iii, 1–60.

1972a. The ascidians of South Australia I. Spencer Gulf, St. Vincent Gulf and Encounter Bay. *Trans. R. Soc. S. Aust.* **96**(1): 1–52.

1972b. The ascidians of South Australia II. Eastern Sector of the Great Australian Bight and Investigator Strait. *Trans. R. Soc. S. Aust.* **96**(4): 165–96.

1972c. Some sublittoral ascidians in Moreton Bay and their seasonal occurrence. *Mem. Qd Mus.* **16**(2): 233–60.

1972d. Notes on some ascidians from Port Jackson, Botany Bay and Port Hacking NSW. *Proc. Linn. Soc. N.S.W.* **97**(4): 241–57.

1972e. The fauna of the Gulf of Carpentaria: Ascidiacea (Chordata : Tunicata). *Fish Notes Qd* (n.s.) **2**: 39–54.

1974. The evolution and distribution of Australian tropical Ascidiacea. *In* 'Proceedings Second International Coral Reef Symposium' Great Barrier Reef 1973 vol. 1 p. 406–23 (Great Barrier Reef Committee: Brisbane).

1975. The ascidians of South Australia III. Northern sector of the Great Australian Bight and additional records. *Trans. R. Soc. S. Aust.* **99**(1): 1–20.

1976. Ascidian fauna of Western Port Bay, Victoria and a comparison with that of Port Phillip Bay. *Mem. natn. Mus. Vict.* **37**: 53–96.

1980. Algal-bearing didemnid ascidians in the Indo-West Pacific. *Mem. Qd Mus.* **20**: 1–47.

1981. The ascidians of the reef flats of Fiji. *Proc. Linn. Soc. N.S.W.* **105**(3): 147–212.

1982a. Didemnid-algal symbiosis: algal transfer to a new host generation. *In* 'Proceedings Fourth International Coral Reef Symposium' Manila 1981 vol. 2 p. 721–3 (University of the Philippines: Quezon City).

1982b. Replication in the Ascidiacea: an adaptive strategy in the coral reef environment. *In* 'Proceedings Fourth International Coral Reef Symposium' Manila 1981 vol. 2. p. 725–33 (University of the Philippines: Quezon City).

1983. Two new genera of didemnid ascidians from tropical Australian waters. *Beagle* **1**(2): 13–19.

1985. The Australian Ascidiacea Pt 1. Phlebobranchia and Stolidobranchia. *Mem. Qd Mus.* **23**: 1–440.

1989. Form and Function in the Ascidiacea. *Bull. mar. Sci.* **45**(2): 253–276.

Kott, P., and Goodbody, I. 1982. The ascidians of Hong Kong. *In* Morton, B.S. and Tseng, C.K. (eds) 'Proceedings of the First International Marine Biological Workshop: the flora and fauna of Hong Kong and Southern China' vol. 1, p. 503–54 (Hong Kong University Press: Hong Kong).

Kott, P., Parry, D.L. and Cox, G. 1984. Prokaryotic symbionts with a range of ascidian hosts. *Bull. mar. Sci.* **34**(2): 308–12.

Kowalevsky, A. 1874. Ueber die Knospung der Ascidien. *Arch. mikrosk. Anat. EntwMech.* **10**: 441–70.

Kupffer, C.W. 1875. Tunicata. *In* 'Jahresb. Commission deutschen Meeren in Kiel' 1872–73 vol. 2 p. 197–228 (Berlin).

Lafargue, F. and Kniprath, E. 1978. Formation de spicules de Didemnidae (ascidies composeés). 1. L'apparition des spicules chez l'oozooide après la métamorphose. *Mar. Biol.* **45**: 175–84.

Lahille, F. 1887. Sur la classification des tuniciers. *C.r. hebd. Seanc. Acad. Sci., Paris* **102**: 1573–5.

1888. Etude systématique des tuniciers. *C.r. Ass. fr. Avanc. Sci.* **1887**(2): 667–77.

1890. 'Récherches sur les tunicies des côtes de France' (Toulouse) 330 pp.

Lesson, R.P. 1830. Zoologie. *In* 'Voyage autour du monde sur *La Coquille* pendant 1882–1825' vol. 2(1) p. 256–79, 433–40 (Paris).

Linnaeus, C. 1767. 'Systema Naturae' 12th ed. vol. 2, pp. 1087, 1089, 1294, 1295, 1319 (Stockholm).

Macdonald, J.D. 1858. Anatomical observations on a new form of compound tunicata (*Chondrostachys*). *Ann. Mag. nat. Hist.* (3)**1**: 401.

Mcdonald, M. 1889. Distribution of duplicate sets of marine invertebrates, 1879–1886. *Rep. U.S. Fish Comm.* **14**: 843–63.

Michaelsen, W. 1898. Vorläufige Mitteilung über einige Tunicaten aus dem Magalhaenischen Gebiet sowie von Süd-Georgien. *Zool. Anz.* **21**: 363–71.

1904. Revision der compositen Styeliden oder Polyzoinen. *Jb. hamb. wiss. Anst.* **21**(2): 1–124.

1907. Tunicaten. *In* 'Ergebnisse der Hamburger Magalhaensischen Sammelreise' vol. 8(5) p. 1–84 (L. Friederichsen and Co: Hamburg).

1914. Ueber einige west-afrikanische Ascidien. *Zool. Anz.* **43**: 423–32.

1915. Tunicata. *In* 'Beiträge zur Kenntnis der Meeresfauna West Afrikas' p. 325–518 (Hamburg).

1919. Die Krikobranchen Ascidien des westlichen Indischen Ozeans: Claveliniden und Synoiciden. *Jb. hamb. wiss. Anst.* 36: 71–102.

1920. Ascidiae Krikobranchiae des Roten Meeres: Clavelinidae und Synoicidae. *In* 'Expedition S.M. Schiff *Pola* in das Rote Meer, nördliche und südliche Hälfte 1895/96–1897/98' Zoologische Ergebnisse xxxiii. *Denkschr. Akad. Wiss. Wien.* **97**: 1–37.

1923. Neue and altbekannte Ascidien aus dem Reichsmuseum zu Stockholm. *Mitt. zool. StInst. Hamb.* **40**: 1–60.

1924. Ascidiae Krikobranchiae von Neuseeland, den Chatham und den Auckland Inseln. *Vidensk. Meddr dansk naturh. Foren.* **77**: 263–434.

1930. Ascidiae Krikobranchiae. *Fauna Südwest-Aust.* **5**(7): 463–558.

1934. The ascidians of the Cape Province of South Africa. *Trans. R. Soc. S. Afr.* **22**(2): 129–63.

Millar, R.H. 1953a. *Ciona. L.M.B.C. Mem. typ. Br. mar. Pl. Anim.* **35**: 1–123.

1953b. On a collection of ascidians from the Gold Coast. *Proc. zool. Soc. Lond.* **123**(11): 277–325.

1955. On a collection of ascidians from South Africa. *Proc. zool. Soc. Lond.* **125**(1): 169–221.

1960. Ascidiacea. '*Discovery*' *Rep.* **30**: 1–160.

1962. Further descriptions of South African ascidians. *Ann. S. Afr. Mus.* **56**(7): 113–221.

1963a. Australian ascidians in the British Museum (Natural History). *Proc. zool. Soc. Lond.* **141**(4): 689–746.

1963b. The larva and affinities of the ascidian *Sigillina vasta* Millar. *Ann. Mag. nat. Hist.* 6(3): 204–207.

1964. South African ascidians collected by Th. Mortensen with some additional material. *Vidensk. Meddr dansk naturh. Foren.* **12**: 159–180.

1966a. Ascidiacea, Port Phillip Survey. *Mem. natn. Mus. Vict.* **27**: 357–75.

1966b. Tunicata. Ascidiacea. *In* 'Marine Invertebrates of Scandinavia' vol. 1 (Scandinavian University Books: Oslo) 123 pp.

1970. Ascidians, including specimens from the deep sea, collected by the R.V. *Vema* and now in the American Museum of Natural History. *Zool. J. Linn. Soc.* **49**: 99–159.

1971. The biology of ascidians. *Adv. mar. Biol.* **9**: 1–82.

1975. Ascidians from the Indo-West Pacific region in the Zoological Museum, Copenhagen (Tunicata : Ascidiacea). *Steenstrupia* **3**(20): 205–336.

1977. Ascidians (Tunicata : Ascidiacea) from the north-eastern Brazilian Shelf. *J. nat. Hist.* **11**(2): 169–223.

1978. Ascidians from the Guyana Shelf. *Neth. J. Sea Res.* **12**(1): 99–106.

1982. The marine fauna of New Zealand. *Mem. N.Z. Ocean. Instit.* **85**: 1–117.

Milne-Edwards, H. 1842. Observations sur les ascidies composées des côtes de la Manche. *Mém. Acad. Sci. inst. Fr.* **18**: 217–326.

Monniot, C. 1969a. Ascidies récoltées par *La Thalassa* sur la pente du plateau continental du Golfe de Gascogne (3–12 août 1967). *Bull. Mus. natn. Hist. nat., Paris* (sér. 2) **41**(1): 155–86.

1969b. Ascidies récoltées par *La Thalassa* sur la pente du plateau continental du Golfe de Gascogne (18–25 Octobre 1968). *Bull. Mus. natn. Hist. nat., Paris* (sér. 2) **41**(1): 1131–45.

1970. Ascidies phlebobranches et stolidobranches. Campagne de *La Calypso* au large des côtes Atlantiques de l'Amérique du sud (1961–62), 17. *Annls Inst. Oceangr. Monaco* **47**: 33–59.

Monniot, C. and Monniot, F. 1973. Ascidies abyssal récoltées au cours de la campagne océanographique Biaçores par *Le Jean Charcot*. *Bull. Mus. natn. Hist. nat. Paris* (sér. 3) **93**(121): 389–475.

1974. Ascidies abyssales de l'Atlantique récoltées par *Le Jean Charcot* (Campagnes Naratlante, Walda, Polygas A). *Bull. Mus. natn. Hist. nat. Paris* (sér. 3) **154**(226): 721–86.

1977. Tuniciers benthiques profonds du nord-est Atlantique. Résultats des campagnes Biogas. *Bull. Mus. natn. Hist. nat. Paris* (sér. 3) **466**(323): 695–720.

1983. Ascidies antarctiques et subantarctic: morphologie et biogéographe. *Mém. mus. natn. Hist. nat. Paris*, sér. A. Zool. **125**: 1–168.

1987. Les ascidies de Polynésie française. *Mém. Mus. natn. Hist. nat. Paris* **136**: 1–155.

Monniot, F. 1988. Ascidies de Nouvelle-Calédonie V. Polycitoridae du lagon. *Bull. Mus. natn. Hist. nat. Paris* (sér. 4) **10**(A2): 197–235.

Mueller, O.F. 1776. 'Zoologiae Danicae' p. 224–26 (Prodromus: Copenhagen).

Nakauchi, M. 1960. On the occurrence of *Archidistoma aggregatum* (a colony forming ascidian) in the Pacific waters. *Publs. Seto mar. biol. Lab.* **8**(2): 223–8.

1966. Budding and growth in the ascidian, *Archidistoma aggregatum*. *Reps Usa Mar. biol. Stat.* **13**(1): 1–10.

Nishikawa, T. 1980. Ascidians from the coast of the Kii Peninsula, Middle Japan, with descriptions of two new species. *Mem. natn. Sci. Mus.* **13**: 97–111.

1984. Ascidians from the Truk Islands, Ponape Island and Majuro Atoll (Tunicata, Ascidiacea). *Proc. Jap. Soc. syst. Zool.* **27**: 107–40.

Nishikawa, T. and Tokioka, T. 1976. Contributions to the Japanese ascidian fauna XXIX. Notes on some clavelinids from the Japanese waters. *Publs Seto mar. biol. Lab.* **23**(1,2): 63-83.

Nott, J.T. 1892. On the composite ascidians of the North Shore Reef. *Trans. N.Z. Instit.* **24**: 305–34.

Oka, A. 1912. On *Cyathocormus mirabilis* n.gen., n.sp., the type of a new family of compound ascidians from Japan. *J. Coll. Sci. imp. Univ. Tokyo* **32**(12): 1-30.

1926. On a new genus of compound ascidians (*Syndiazona* nov. gen.). *Proc. imp. Acad. Japan* **2**: 133–5.

1927a. Ueber *Dendroclavella*, eine neue Gattung von sozialen Ascidien. *Proc. imp. Acad. Japan* **3**(8): 555–7.

1927b. Ueber zwei neue *Rhopalaea*-Arten aus Japan. *Proc. imp. Acad. Japan* **3**: 681–3.

1927c. Zur Kenntnis der japanischen Botryllidae. *Proc. imp. Acad. Japan* **3**(9): 607–9.

1927d. Ascidians. *In* 'Figuraro de Japanaj Bestoj' p. 494–8.

1930. Ueber eine neue langgestielte Synascidie aus der Bucht von Sagami. *Proc. imp. Acad. Japan* **4**: 303–5.

1933. Ein Fall von Kolonialknospung bei einer Synascidie. *Proc. imp. Acad. Japan* **9**: 436–8.

1934. Ueber *Clavelina coerulea* n.sp., die erste von Japan bekannt gewordene *Clavelina*. *Proc. imp. Acad. Japan* **10**(6): 365–6.

Parry, D.L. 1984. Chemical properties of the test of ascidians in relation to predation. *Mar. Ecol. Prog. Ser.* **17**: 279–82.

1987. 'Selected Chemistry of the Ascidian' (Ph.D. thesis: University of Queensland) 221 pp.

Pérès, J.M. 1948. Sur une collection d'ascidies de la zone intercotidale de Dakar. *Bull. Mus. natn. Hist. nat. Paris* (sér. 2) **20**(1): 91.

Pfeffer, G. 1889. Zur Fauna von Süd-Georgien. *Mitt. naturh. Mus. Hamb.* **6**(5): 3–4.

1890. Die niedere Thierwelt des antarktischen Ufergebietes. *In* Neumayer, G. (ed.) 'Die Deutschen Expeditionen und ihre Ergebnisse' vol. 2. p. 455–572 (Berlin).

Philippi, R.A. 1843. *Rhopalaea* ein neues Genus der einfachen Ascidien. *Arch. Anat. Physiol.* **1**: 45–7.

Pisano, A., Rengel, D. and Bustuoabad, O. 1971. Finding of *Ciona robusta* in Argentine Seas. *Ann. Inst. Mus. Zool. Univ. Napoli* **19**(9): 1–10.

Plante, R. and Vasseur, P. 1966. Sur une collection d'ascidies de la région de Tuléar (côte sud-ouest de Madagascar). *Annales de l'Université de Madagascar* Série Sciences de la Nature et Mathématiques, no **4**: 143–52, 4 pls.

Pizon, A. 1908. Ascidies d'Ambione. *Rev. Suisse Zool.* **16**: 195–248.

Pratt, H.S. 1916. Tunicata. *In* 'A manual of the common invertebrate animals exclusive of insects' p. 655–71 (Chicago).

Quoy, J. and Gaimard, P. 1834. Mollusques. *In* 'Voyages de découvertes de *l'Astrolabe* 1826–29', Zoologie vol. 3 p. 559–626; vol. 4 p. 304–6.

Renier, S.A. 1804. 'Prospetto della classe dei Vermi' pp. xv–xxvii (Padua); *fide* Porro, C. 1840, 'Nota per una Bibliografia Malacologie, Series III Geografica no. 1–4, p. i–iii and numbered columns 27–130.

Ridgeway, R. 1886. 'A nomenclature of colours for naturalists and compendium of useful knowledge for ornithologists' (Little, Brown and Co.: Boston) 129 pp.

Ritter, W.E. 1900. Some ascidians from Puget Sound. Collections of 1896. *Ann. N.Y. Acad. Sci.* **12**: 589–616.

1903. The structure and affinities of *Herdmania claviformis*, the type of a new genus and family of ascidians from the coast of California. *In* 'Mark Anniversary Volume' p. 237–61, pls xvii, xix (Henry Holt and Co.: New York).

1913. The simple ascidians from the north-eastern Pacific in the collection of the United States National Museum. *Proc. U.S. natn. Mus.* **45**: 427–505.

Ritter, W.E. and Forsyth, R.A. 1917. Ascidians of the littoral zone of southern California. *Univ. Calif. Publs Zool.* **16**: 439–512.

Roule, L. 1884. Récherches sur les ascidies simples des côtes de Provence I. Phallusiadées. *Annls Mus. Hist. nat. Marseille* **2**(1): 1–270.

Saffo, M.B. 1978. Studies on the renal sac of the ascidian *Molgula manhattensis*. *J. Morph.* **155**(3): 287–310.

Salensky, W. 1893. Morphologische Studien an Tunicaten II. Ueber die Metamorphose der *Distaplia magnilarva*. *Morph. Jahrb.* **20**: 449–542.

Salfi, M. 1925a. Le sinascidie del gen. *Sycozoa* raccolte dal Cap. G. Chierchia duranteil viaggia circumnavigazione della R. Corvetta *Vettor Pisani* negli anni 1882–1885. *Annuar. R. Mus. zool. R. Univ. Napoli* (nuovo ser.) **5**(2): 1–9.

1925b. La fissazione della larva e la genesi della colonia in *Holozoa magnilarva* (Della Valle). *Boll. Soc. Nat. Napoli* **37**: 224–30.

1926. Ulteriori osservazioni sulle sinascidie del gen. *Sycozoa* Less. della *Vettor Pisani*. *Annuar. R. Mus. zool. R. Univ. Napoli* (nuovo ser.) **5**(16): 1–10.

1927. Note descrittive e biologiche su due ascidie del Golfodi Napoli. *Pubbl. Staz. zool. Napoli* **8**: 273–85.

1928. Richerche sulla biologia delle ascidie del Golfo di Napoli. *Ricerche di Morfologia e Biologia Animale* **1**(2): 8–370.

1933. Le recenti richerche sui fenomeni di riproduzione asessuata dei tunicati (English resumé p. 200). *Archo zool. ital.* **19** (suppl): 121–201.

Sars, M. 1851. Beretning om en i Sommeren 1849, foretagen zoologiske Reise i Lofoten og Finmarken. *Nytt Mag. Naturvid.* **6**: 121–211.

1859. Bidrag til en skildering af den arktiske molluskfauna ved Norges nordlige Kyst. *Forh. VidenskSelsk. Krist.* **1858**: 34–87.

Savigny, J.C. 1816. 'Mémoires sur les animaux sans vertèbres' pt. 2, p. 1–239 (Paris).

Saville-Kent, W. 1897. Marine Miscellanea. *In* 'The Naturalist in Australia' p. 215–51 (Chapman and Hall: London).

Schmeltz, J.D.E. 1879. 'Catalogue of the Museum Godeffroy' cat. 7, p. 89–90.

Seeliger, O. 1893–1907. Appendicularien und Ascidien (Tunicata, Manteltiere). *In* Bronn, H.G. 'Klassen und Ordnungen des Tier-Reichs' vol. 3 suppl. p. 26–80, 385–1280 (C.F. Winter: Leipzig). Continued by Hartmeyer 1909–1911.

Shepherd, S.A. 1983. The epifauna of megaripples: species adaptations and population responses to disturbance. *Aust. J. Ecol.* **8**: 3–8.

Sluiter, C.P. 1885. Ueber einige einfachen Ascidien von der Insel Billiton. *Nat. Tijdschr. Nederl. Ind.* **45**: 160–232.

1895. Tunicaten. *In* Semon, R. (ed.) 'Zoologische Forschungsreisen in Australien und dem Malagischen Archipel'. *Denkschr. med.-naturw. Ges. Jena* **8**: 163–86. Nachtrag zu den Tunicaten: 325–6.

1898. Tuniciers récueillis en 1896 par *La Chazalie* dans la Mers des Antilles. *Mém. Soc. zool. Fr.* **11**: 5–34.

1900. Tunicaten aus dem Stillen Ocean. *Zool. Jb.* (Systematik) **13**: 1–35.

1904. Die Tunicaten der *Siboga*-Expedition Pt. I. Die socialen und holosomen Ascidien. *Siboga Exped.* **56A**: 1–126.

1906. 'Tuniciers de l'Expédition antarctique Francaise 1903–05' (Masson: Paris).

1909. Die Tunicaten der *Siboga* Expedition Pt. 2. Die merosomen Ascidien. *Siboga Exped.* **56B**: 1–112.

1919. Ueber einige alte und neue Ascidien aus dem Zoologischen Museum von Amsterdam. *Bijdr. Dierk.* **21**: 1–12.

Spencer, R.S. 1956. Studies in Australian estuarine hydrology II. The Swan River. *Aust. J. mar. Freshw. Res.* **7**: 193–253.

Stimpson, W. 1852. Several new ascidians from the coast of the United States. *Proc. Boston Soc. nat. Hist.* **4**: 228–32.

1854. Synopsis of the marine Invertebrata of Grand Manan; or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithson. Contr. Knowl.* **6**(5): 1–68.

1860. A trip to Beaufort, N. Carolina. *Am. J. Sci.* (2)**29**: 442–445.

Sumner, F.B., Osburn, R.C., and Cole, L.J. 1913. A biological survey of the waters of Woods Hole and vicinity. *Bull. U.S. Bureau of Fisheries* **31**: 1–860.

Tokioka, T. 1942. Ascidians found on the mangrove trees in Iwayama Bay, Palao. *Palao trop. biol. Stn. Stud.* **2**(3): 497–507.

1950. Ascidians from the Palao Is (1). *Publs Seto mar. biol. Lab.* **1**(3): 115–50.

1951a. The fauna of Akkeshi Bay. XVIII Ascidia. (Contribution to Japanese ascidian fauna III). *Publs Akkeshi mar. biol. Stn* **1**: 1–24.

1951b. Contributions to Japanese ascidian fauna IV. Notes on some ascidians collected in Osaka Bay (1). *Publs Seto mar. biol. Lab.* **1**(4): 169–82.

1952. Ascidians collected by Messrs Renzi Wada and Seizi Wada from the Pearl Oyster bed in the Arafura Sea in 1940. *Publs Seto mar. biol. Lab.* **2**(2): 91–142.

1953. 'Ascidians of Sagami Bay' p. 1–313, 79 pls (Iwanami Shoten: Tokyo).

1954a. Contributions to Japanese ascidian fauna VII. Invertebrate fauna of the intertidal zone of the Tokara Islands. VII Ascidians. *Publs Seto mar. biol. Lab.* **3**(3): 239–64.

1954b. Contributions to Japanese ascidian fauna IX. Redescriptions of Oka's species found in 'Figuraro de Japanaj Bestoj'. *Publs Seto mar. biol. Lab.* **4**(1): 69–75.

1954c. Contributions to Japanese ascidian fauna X. Notes on some ascidians collected in Osaka Bay (2). *Publs Seto mar. biol. Lab.* **4**(1): 75-98.

1955a. Contributions to Japanese ascidian fauna XI. Sporadic memoranda (2). *Publs Seto mar. biol. Lab.* **4**(2,3): 205-22.

1955b. Ascidians from the Palao Islands (II). *Publs Seto mar. biol. Lab.* **5**(1): 43-57.

1958. Contributions to Japanese ascidian fauna XII. Sporadic memoranda (3). *Publs Seto mar. biol. Lab.* **6**(3): 313-25.

1959. Contributions to Japanese fauna XIII. Sporadic memoranda (4). *Publs Seto mar. biol. Lab.* **7**(2): 223-36.

1962. Contributions to Japanese ascidian fauna XIX. Additions to Japanese ascidian fauna with notes on two already known species. *Publs Seto mar. biol. Lab.* **10**(2): 260-82.

1963. Contributions to Japanese ascidian fauna XX. The outline of Japanese ascidian fauna as compared with that of the Pacific coast of North America. *Publs Seto mar. biol. Lab.* **11**(1): 131-56.

1967a. Pacific Tunicata of the United States National Museum. *Bull. U.S. natn. Mus.* **251**: 1-242.

1967b. On a small collection of ascidians from the vicinity of Nhatrang, Vietnam. *Publs Seto mar. biol. Lab.* **14**(5): 391-402.

1967c. Contributions to Japanese ascidian fauna XXII. Ascidians from Sado I (2). *Publs Seto mar. biol. Lab.* **15**(3): 239-44.

1970. Ascidians from Mindoro Island, the Philippines. *Publs Seto mar. biol. Lab.* **18**(2): 75-107.

1971. A new species of *Rhopalaea* from the Pacific Coast of Costa Rica (Tunicata, Ascidiacea). *Publs Seto mar. biol. Lab.* **19**(2,3): 119-22.

TOKIOKA, T., AND NISHIKAWA, T. 1975. Contributions to Japanese ascidian fauna XXVII. Some ascidians from Okinawa, with notes on a small collection from Hong Kong. *Publs Seto mar. biol. Lab.* **22**(5): 325-41.

1976. Contributions to the Japanese ascidian fauna XXX. Further notes on Japanese clavelinids. *Publs Seto mar. biol. Lab.* **23**(3-5): 341-50.

TRASON, W.B. 1957. Larval structure and development of the oozooid in the ascidian *Euherdmania claviformis*. *J. Morph.* **100**(3): 510-26.

1963. The life cycle and affinities of the colonial ascidian *Pycnoclavella stanleyi*. *Univ. Calif. Publs Zool.* **65**(4): 283-326.

TRAUSTEDT, M.P.A. 1880. Oversight over de fra Danmark og dets nordlige Bilande kjendte Ascidiae Simplices. *Vidensk. Meddr dansk Naturh. Foren.* 1879-1880: 397-443.

1882. Vestindiske Ascidiae Simplices, Forste Afdeling. Phallusiadae. *Vidensk. meddr dansk naturh. Foren.* **1881**: 257-88.

VAN NAME, W.G. 1902. The ascidians of the Bermuda Islands. *Trans. Conn. Acad. Arts Sci.* **11**: 325-412.

1912. Simple ascidians of the coasts of New England and neighbouring British Provinces. *Proc. Boston Soc. nat. Hist.* **34**: 439-619.

1918. Ascidians of the Philippines and adjacent waters. *Bull. U.S. natn. Mus.* **100**(1): 49-174.

1921. Ascidians of the West Indian region and south eastern United States. *Bull. Am. Mus. nat. Hist.* **44**: 283-494.

1945. The North and South American ascidians. *Bull. Am. Mus. nat. Hist.* **84**: 1-476.

VASSEUR, P. 1969. Deuxième contribution a l'étude, des ascidies de Madagascar région de Tuléar. *Bull. Mus. natn. Hist. nat., Paris* **40**(5): 912-33.

VERRILL, A.E. 1871. Descriptions of some imperfectly known and new ascidians from New England. *Am. J. Sci.* (3)**1**: 54-8, 93-100, 211-2, 288-94, 443-6.

1872a. Marine fauna of Eastport. *Bulletin Essex Institute, Maine* **3**: 2-6.

1872b. Recent additions to the molluscan fauna of New England and the adjacent waters, with notes on the other species. *Am. J. Sci.* (ser. 3) **3**: 209-14, 281-90, pls. 6-8.

1873-1874. Results of recent dredging expeditions on the coast of New England. *Am. J. Sci.* (ser. 3) **5**: 1-16, 98-110; **6**: 435-41; **7**: 38-46, 131-8, 405-14, 498-505, 608, pls. 6-8.

1880. Occurrence of *Ciona ocellata* (*Ascidia ocellata* Agassiz) at Newport, R.I. *Am. J. Sci.* (ser. 3) **20**: 251-2.

VERRILL, A.E. AND SMITH, S.I. 1873. Report on the invertebrate animals of Vineyard Sound and adjacent waters with an account of the physical features of the region. *Rep. U.S. Fish. Comm.* **1**: 296-778, pls 1-38, 3 maps.

WATANABE, H. AND TOKIOKA, T. 1973. On a new species of *Clavelina* from Japan, with remarks on its mode of budding. *Publs Seto mar. biol. Lab.* **21**(2):99-107.

WHITEAVES, J.F. 1901. Catalogue of the marine invertebrata of eastern Canada. *Geol. Surv. Canada*, publ. no. **722**: 265-71.

INDEX TO TAXA

Page numbers of taxon descriptions and figures appear in **bold**

Amaroucium,
  anomalum, 79
  distomoides, 134
Amphicarpa, 165
Aplidie,
  cerebriforme, 143
  pedunculatum, 147
Aplidium, 13
  lobatum, 179
  distomoides, 134
  pedunculatum, 147 153
  triggiensis, 8
Aplousobranchia, **18-20**
Araneum, 21
Archiascidia, 35 67
  neapolitana, 67
Archidistoma, 76 162 163
  aggregatum, 163
  richeri, 73
  rubripunctum, 73
Ascidia,
  canina, 21
  intestinalis, 21
  lepadiformis, 35
  ocellata, 21
  pulchella, 21
  tenella, 21
Aseidiidae, 13 21
Atapozoa, 82
  deerrata, 106
  fantasiana, 92
  marshi, 87 89
  mirabilis, 108
Atopogaster aurantiaca, 159
Atriolum, 10 19 83

Botryllinae, 10
Botrylloides magnicoecus, 10
Brevicollus, 4 14 16 162 163 **236**
  tuberatus, 8 236 **237-8** **254**

Chondrostachys, 35 42
  cylindrica, 42
  macdonaldi, 42
Ciona, 8 12 13 14 15 16 18 19 20 **21** 22 26 34
  antarctica, 21
  canina, 21
  diaphanaea, 22
  fascicularis, 22
  gelatinosa, 22
  imperfecta, 21
  indica, 21 24 26
  intestinalis, 20 **21-4** **239**
  intestinalis longissima, 21 34
  intestinalis gelatinosa, 21 34
  ocellata, 21
  pulchella, 22
  robusta, 22
  savignyi, 21 24
  sociabilis, 21
  tenella, 21
Cionidae, 4 9 13 14 18 **20-1** 24
Clavelina, 16 18 **35-8** 39 63 66 67 70 79 80 156
  arafurensis, 35 36 37 **38-9** 170 **238**
  australis, 16 35 36 37 **39-41** 45 50 53 61 63 **240**
  baudinensis, 16 17 33 34 35 36 37 **41-2** 58 60 61 **240**
  brasiliensis, 16 46
  claviformis, 79
  coerulaea, 36 51 53
  cyclus, 36 54 55
  cylindrica, 14 35 36 37 **42-5** 50 53 63 66 70 **240**
  dagysa, 12 16 34 35 36 37 **45-6** 50 57 58 **241**
  detorta, 71
  diminuta, 73
  elegans, 36 39 48 63
  enormis, 36 41 48
  fecunda, 16 35 36 37 42 **47-8**
  flava, 38
  meridionalis, 12 16 18 33 35 36 37 46 **48-50** 51 58 **241**
  miniata, 12 18 38 46 50 57
  mirabilis, 35 36 37 **50-1**
  minuta, 33
  moluccensis, 14 15 16 35 36 37 38 41 44 45 50 **51-3** 54 61 63 **241**
  nana, 70 71
  nigra, 14 35 36 37 53 **53-5** **242**
  nodula, 73
  obesa, 38 48
  oliva, 16 18 35 36 37 38 39 **55-7** **242**
  ostrearium, 12 18 33 35 36 37 46 48 50 **57-8** **242**
  pseudobaudinensis, 16 33 35 36 37 39 41 42 51 **58-61** 63 **242**
  robusta, 15 16 35 36 37 41 48 51 53 **61-3** **242**
  roseola, 157
  sigillaria, 79
  viola, 12 36 38 57 63
Clavelinidae, 4 8 9 10 12 13 14 15 16 17 18 19 20 21 24 **33-5** 63 66 67 81 82 83 84 156 162
Colella,
  claviformis, 34 66 79
  cyanea, 89
  elongata, 205
  incerta, 143
  murrayi, 146

  pedunculata, 147 153
  perrieri, 155
  plicata, 143
  pulchra, 149
  quoyi, 153
  ramulosa, 153
  sigillinoides, 153
  tenuicaulis, 149 152
  thompsoni, 64
  umbellata, 153
Corellidae, 13
Cyathocormus, 84 137 139
  mirabilis, 137
Cystodytes, 8 10 13 15 17 18 69 162 163 **178** 183
  aucklandicus, 179
  ceylonensis, 179
  cretaceous, 179
  dellachiajei, **179-83** **252**
  draschei, 179
  durus, 179
  fuscus, 182
  hapu, 179 183
  mucosus, 182 183
  perspicuus, 179
  philippinensis, 179 182
  punctatus, 182 183
  violaceus, 179
  violatinctus, 182

Diazona, 24 25
  gigantea, 157
  violacea, 25
Diazonidae, 4 6 8 9 12 13 14 15 16 18 19 20 24 **24-5** 25 31 33 34 66 83 156 162
Didemnidae, 4 7 8 9 10 12 13 14 15 17 18 19 20 83 109 126
Diplosoma, 16
  macdonaldi, 8
  multipapillata, 8
Distaplia, 8 10 12 13 14 15 16 17 18 19 81 82 83 84 **109-13** 110 126 135 137 156 159 162 178 183 236
  australiensis, 110 111 112 **113-5** 120 121 **247**
  bursata, 114
  capensis, 111
  cerebriforme, 143
  cuscina, 111 112 113 **115-6** 118 120 122 125 132 133
  cylindrica, 126
  distomoides, 134
  dubia, 111 112 **116-8** 122 **247**
  durbanensis, 111
  fasmeriana, 133
  florida, 13 111 112 **118-9** 120 125 133 **247**
  japonica, 116
  magnilarva, 81 127
  mikropnoa, 111 127 129
  muriella, 110 111 112 **119-21**
  occidentalis, 8 16 110
  pallida, 111 112 118 119 **121-2** 122 124 130 132 133 135 **247**
  prolifera, 111 112 **122-4** 130 135
  racemosa, 111 112 113 120 **123** **124-5**
  regina, 111 112 120 **123** **125**
  retinaculata, 15 81 82 111 112 **125-6** 129 133 134 135
  skoogi, 111
  smithi, 110 114
  stylifera, 111 112 114 124 125 **127-9** 130 132 134 135 **247**
  systematica, 110 113 124
  tahiluero, 113 116
  tokioka, 111 112 119 122 124 **129-30** 131 132
  vallii, 110 111 113 114 115 116
  violetta, 110 111 112 115 121 124 129 130 **130-2**
  viridis, 13 111 112 118 119 121 122 125 126 130 **132-3** **248**
  yezoensis, 125
Distoma,
  caerulea, 89
  deerratum, 105 106 234
  dellechiajei, 178 179
  laysani, 214
  molle, 220
  parva, 214
  rubrum, 188
Distomidae, 82 83
Distomus, 165
Dumus areniferus, 79

Ecteinascidia
  crassa, 26
  fusca, 26
  solida, 26
Ecteinascidia (? Rhopalopsis) solida, 26
Enterogona, 4 9 18
Euclavella, 14 19 34 66 67 **79**
  claviformis, 17 66 **79-80** 86 **245**
Eucoelium hospitiolum, 183
Eudistoma, 6 8 9 10 13 14 15 16 17 19 69 92 100 101 162 163 178 183 **188-94** 203 212 222 230 234 236 238
  album, 214
  amplum, 188 190 192 **194-6** 222 225 228 **253**
  anaematum, 190 193 **196-7** 208 218 224
  angolanum, 191 192 194 **197-9** 203 225 228
  aureum, 189 193 **199-200** 226
  bulbatum, 163 191 192 193 **200-1**
  caeruleum, 89
  carnosum, 16 191 192 198 199 **201-3** 228
  clarum, 15 162

constrictum, 191 193 **203-4** 220 229 231 **253**
cyanea, 89
cyaneum, 89
desciderata, 163
eboreum, 190 193 **205** 206
elongatum, 15 189 193 204 **205-6** 210 216 231 **253**
fantasiana, 92
fragum, 193
gilboviride, 189 192 194 **206-8** 232 233 **253**
glabrum, 193
glaucum, 162 189 193 194 **208-10** 217 218 224 231
globosum, 189 193 200 204 **210-1** 218 227 231
gracilum, 191 193 **211-2** 216
incubitum, 16 162 190 193 194 **212-3**
laysani, 15 163 189 193 194 204 206 212 **214-6** **253**
loricatum, 193 194
maculosum, 162 190 193 200 210 **216-7** 225 226 231 236 **254**
malum, 189 193 196 200 **217-8** **291**
marianense, 209 217 226
microlarvum, 191 193 204 **218-20** 231
miniacum, 193
molle, 8 220
multiperforatum, 193 228
murrayi, 163
muscosum, 162 190 193 196 198 208 210 217 **220-2** 224 228 232
olivaceum, 15 162 208 210 214
ovatum, 16 191 192 203 204 **222-4** 225 229 232 233
parvum, 214 216
pratulum, 190 193 196 208 **223** **224**
purpureum, 16 162 190 193 196 208 217 **225-6** 232
pyriforme, 191 192 196 199 200 216 222 **226-7** 229
reginum, 192 198 **227** **228** **254**
renieri, 216 226
rigidum, 208 209 231 232
ritteri, 8
rubrum, 194
sabulosum, 191 192 204 222 226 **229** **254**
segmentatum, 149 216 233
snakabri, 198
stellatum, 194
superlatum, 162 170 189 193 210 **229-31**
tigrum, 190 193 208 210 217 218 222 **231-2**
toealensis, 193 194 216
tokarae, 194 210
tumidum, 189 192 **232-3**
viride, 100 101 210
viridis, 100
vitiatum, 196
  vulgare, 222
Euherdmania, 6 8 12 13 14 15 17 19 38 53 67 81 84 86 98 156
  claviformis, 86
  dentatosiphonis, 156
  digitata, 156
Euherdmaniinae, 7 9 10 14 15 17 19 30 31 38 79
Exostoma, 8 9 10 13 20 105 106 162 163 194 **233-4**
  ianthinum, **234-6**

Holozoa,
  cylindrica, 109
  valii, 115
Holozoidae, 4 8 9 10 12 13 14 15 16 18 19 20 66 **81-4** 102 106
Holozoinae, 82 83 162
Homoeodistoma longigona, 33
Hyperiodistoma, 82 162
Hypodistoma, 4 8 9 10 13 14 17 81 82 83 84 86 93 100 102 **105-6** 126 234 236
  deerratum, 82 105 **106-8** 109 194 **246**
  ianthinum, 234 236
  mirabile, 82 105 106 **108-9** **246**
  vastum, 15 82 100 105 106 108 109 234 236
Hypsistozoa, 8 12 13 14 16 17 18 81 82 84 **133-4** 135 137 236
  distomoides, 122 129 133 **134-5** **248**
  fasmeriana, 122 133 135
  obscura, 134

Leptobotrylloides dubium, 116
Leptoclinides, 10 83

Molgula, 8
Molgulidae, 9 13

Neodistoma, 10 14 18 82 84 **135** 236
  mammillatum, **135-7** **249**
Nephtheis, 14 19 33 35 60 **63** 79
  faciformis, 64
  fascicularis, 14 55 **63-6** **243**
  malayensis, 64
  thompsoni, 64

Oxycorynia,
  arenosa, 69
  fascicularis, 63
  pseudobaudinensis, 58

Paessleria, 162
Patridium, 31
  pulvinatum, 31 33
Perophoridae, 13
Phallusia intestinalis, 21
Phlebobranchia, 4 5 8 9 12 13 14 15 18 19 20 21

- Pleurogona, 4
- *Podoclavella*, 35
  - *australis*, 39 44
  - *cylindrica*, 44 51
  - *dagysa*, 45
  - *detorta*, 71
  - *fecunda*, 47
  - *meridionalis*, 48 57 61
  - *moluccensis*, 51 53 61 63
  - *ostrearium*, 57
  - *polycitorella*, 38
  - *procera*, 48 50
- *Polycarpa*, 8
- *Polycitor*, 8 9 10 13 15 16 25 162 163 **165** 183 194 236 238
  - *amplus*, 194 198 199
  - *angolanus*, 197
  - *annulus*, 15 17 162 164 165 **165-7** 170 175
  - *arenaceus*, 222
  - *aurantiacus*, 159 161
  - *calamus*, 164 165 **167-8** 175 **251**
  - *cerasus*, 164 165 **168-9** 175 **251**
  - *circes*, 15 17 162 164 165 167 **169-70** 174 175 177
  - *coalitus*, 106 194
  - *crystallinus*, 165 177 178
  - *discolor*, 194 196
  - *emergens*, 164 165 **170-1** 177
  - *gelatinosa*, 169 170 171
  - *giganteus*, 6 164 165 170 **171-4** 177 178 **251**
  - *gilboviridis*, 206
  - *glaucus*, 208
  - *ianthinus*, 106 194 233 234
  - *irregularis*, 214
  - *laysani*, 214
  - *longitubis*, 104
  - *magalhaensis*, 203
  - *mollis*, 220
  - *nubilus*, 164 165 **174-5 251**
  - *obeliscus*, 164 165 **174 175** 238
  - *paesslerioides*, 197 198 201 203
  - *renziwadai*, 25 169
  - *scaber*, 222
  - *signiferus*, 100 194
  - *subarborensis*, 164 165 171 **175-7**
  - *torosus*, 105 234 236
  - *translucidus*, 16 171 164 165 170 **176 177-8**
  - *violaceus*, 194
  - *vitreus*, 15 162
- *Polycitor (Eudistoma)*,
  - *olivaceum*, 214
  - *paesslerioides*, 201 203
- *Polycitorella*, 4 8 10 13 15 18 162 163 178 **183-4** 204
  - *coronaria*, 183 **184-7** 188 **252**
  - *hospitiolis*, 183
  - *mariae*, 183 184 186 188
  - *orientalis*, 183 **187-8 252**
  - *pallida*, 184 186 188
  - *pérèsi*, 184
  - *setoensis*, 184
- Polycitoridae, 4 7 8 9 10 12 13 14 17 19 20 66 69 81 82 83 106 156 **162-3** 237
- Polycitorinae, 82 83 162
- Polyclinidae, 4 7 8 9 10 12 13 14 15 17 19 20 24 30 38 66 67
- *Polyclinum*, 9 15 24
  - *cylindricum*, 42
  - *giganteum*, 171
  - *globosum*, 171
  - *mikropnous*, 129
  - *nigra*, 98
- *Polydistoma*, 4 8 9 10 13 14 81 82 83 84 **101-2** 105 109 126 236
  - *fungiforme*, 101 **102-3** 105
  - *longitube*, 103 **104-5**
- Polyzoinae, 67
- *Prochloron*, 16
- *Protoholozoa*, 84
- *Protopolyclinum*, 9 15 24 30
  - *claviforme*, 30 31
  - *pedunculatum*, 31
- *Psammaplidium*,
  - *ovatum*, 222
  - *pyriforme*, 226
- *Pseudodiazona*, 13 14 19 24 25 **30-1** 33
  - *abyssa*, 31
  - *claviformis*, **31-3 238**
  - *sabulosa*, 30 31
- *Pseudodistoma*, 15 19 231
- *Pycnoclavella*, 7 9 14 15 34 35 38 66 **67-9** 70 76 79 163
  - *arenosa*, 38 67 68 **69-71** 73 76 **243**
  - *aurantia*, 66 68 69 **71 72** 73 76 **243**
  - *aurilucens*, 66 67 69 70
  - *detorta*, 17 67 68 69 **71-3** 76 **243**
  - *diminuta*, 67 68 69 71 **73-6** 77 78 79 **244**
  - *elongata*, 67 68 69 **76-7** 244
  - *kottae*, 66 67 69 73
  - *minuta*, 66 69 70
  - *stanleyi*, 66 67 69 71
  - *tabella*, 67 68 69 73 76 **77-9 244**
- Pycnoclavellidae, 4 6 8 9 10 12 13 14 15 17 18 19 20 **66-7** 69 79 81 83 84 86 98
- *Pyura*, 13
- Pyuridae, 9 13

- *Rhopalaea*, 12 13 14 18 24 **25-6** 28 30
  - *abdominalis*, 25 29
  - *birkelandi*, 25
  - *crassa*, 24 25 **26-9** 30 **238**
  - *hartmeyeri*, 25 29

  - *macrothorax*, 26 28
  - *neapolitana*, 25 26 28 30
  - *nordgaardi*, 24 25 26 30
  - *norvegica*, 25
  - *piru*, 25 26
  - *sagamiana*, 26
  - *tenuis*, 13 25 26 **29-30**
- *Rhopalopsis*, 26
  - *birkelandi*, 29
  - *crassa*, 26
  - *defecta*, 25 26 28
  - *fusca*, 26 29
  - *neapolitana*, 29
- *Ritterella*, 10 13 15 24 236 237
  - *prolifera*, 216

- *Sigillina*, 4 6 7 8 9 10 13 14 15 16 17 19 81 82 83 **84-7** 98 100 102 105 108 162 163 203 210 231 234 236
  - *australis*, 13 82 84 85 86 87 **87-9** 90 92 96 101 206 **245**
  - *caerulea*, 89 92
  - *coalita*, 106
  - *cyanea*, 29 66 85 86 87 **89-92** 93 96 101 **245**
  - *deerrata*, 106
  - *digitata*, 86 87 93 96 99 100
  - *fantasiana*, 81 82 84 85 86 87 **92-3** 99 100 105 162 231 **246**
  - *grandissima*, 12 15 16 81 84 85 86 87 89 **93-6** 101 170 **246**
  - *magalhaensis*, 198 201 203
  - *mjöbergi*, 4 8 13 17 19 81 84 85 86 87 **96-8**
  - *möbiusi*, 86 87
  - *nigra*, 84 85 86 87 93 **98-100** 162 **231**
  - *psammophorus*, 86 87
  - *signifera*, 85 86 87 89 96 **100-1** 167 194 210 **246**
  - *vasta*, 234
- *Sigillina (Paessleria)*, 201 203
- *Sigillina (Polycitor)*, 106
- *Stereoclavella*, 35
  - *australis*, 39
- Stolidobranchia, 4 5 6 8 9 10 12 13 14 15 18 19 20 67
- *Stomozoa*, 35 156 157
  - *australiensis*, **157-9** 161 **250**
  - *bellissima*, **159-61 250**
  - *murrayi*, 157
  - *roseola*, 156 157 159
- Stomozoidae, 4 8 9 10 13 14 16 19 20 35 **156-7** 162
- Styelidae, 9 13
- *Sycozoa*, 6 8 9 10 12 13 14 15 16 17 19 81 82 83 84 110 **137-40** 162
  - *anomala*, 13 137 138 140 143
  - *arborescens*, 139 140 153
  - *brevicauda*, 16 137 138 **140-2** 146 152
  - *cavernosa*, 138 139 140 **142-3** 149 155 156
  - *cerebriformis*, 82 137 138 139 **143-6** 152 **249**
  - *gaimardi*, 140
  - *georgiana*, 139 140
  - *kanzasi*, 139 140 152
  - *mirabilis*, 140 143
  - *murrayi*, 138 140 **146-7** 156 **250**
  - *pedunculata*, 138 139 140 **147-9** 152 153 155 156 **250**
  - *perrieri*, 155
  - *pulchra*, **2** 16 137 138 139 140 142 147 149 **149-52** 153 155 156 **250**
  - *quoyi*, 153
  - *sedens*, 100
  - *seiziwadai*, 138 139 140 146 147 152 **152-3 154**
  - *sigillinoides*, 137 138 139 140 146 147 149 152 **153-6**
  - *tasmanoides*, 146
  - *tenuicaulis*, 149
  - *umbellata*, 153
- *Synclavella*, 35 61
  - *australis*, 39 58
  - *lessoni*, 58
- *Syndiazona*, 24 25
  - *chinensis*, 25 26 30

- *Tethyum sociabile*, 21
- *Tetrazona*, 162
- *Tylobranchion*, 24 25 30 31
  - *speciosum*, 33